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THE FAMILY ANATIDAE

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A MORE natural grouping of species with a better understanding of their affinities expressed in a simpler taxonomy has been one of our principal objects for many years. Among the most popular groups of birds, the waterfowl, as the Anatidae are known, have perhaps been more arbitrarily classified than any other. Because of the general interest attached to these birds, we have thought that it might be useful to revise the group and to state our views on the relationships within it. Delacour (1933, 1936, 1938) has already published several papers on the subject. But since their appearance our knowledge has advanced considerably, and the present paper is a corrected, expanded, and up-to-date version, in English, of these earlier articles.

For over 20 years Delacour maintained in the park of the Chateau de Clères, in Normandy, the greatest collection of live waterfowl ever gathered. All existing species of swans, geese, tree ducks, and sheldrakes were represented in it; and of all the other ducks, only 26 species were missing. They lived under conditions approaching those of the wild state, and consequently they bred freely and displayed their natural behavior, including their courtship. In addition, we have observed many of the rarer exotic species in their natural habitat, and we have extensively studied museum series at the American Museum and elsewhere.

We also have benefited by the work of many authors, ornithologists, sportsmen, and breeders, particularly by the excellent pioneer studies of Dr. O. Heinroth (1910; 1911; and with M. Heinroth, 1928). For many years, Delacour has exchanged views, notes, and specimens with Dr. K. Lorenz, of Vienna, on the subject of the display and affinities of the Anatidae, with a view to later joint publication. The files kept at Clères were destroyed by a fire in 1939. We know that Dr. Lorenz has since published a paper on the subject, but this is unfortunately not yet available to us (Lorenz, 1941). It will be interesting to compare his conclusions with ours.

The classification of ducks which has been accepted up to the present is more than 50 years old. In spite of criticism by a number

of recent authors, it has been more or less followed in all recent works, such as Phillips' "A Natural History of the Ducks" (1922–26); Peters' "Check-List of Birds of the World" (1931); and the fourth edition of "The A.O.U. Check-List of North American Birds" (1931). In fact, Salvadori's classification in the "Catalogue of Birds in the British Museum" (Vol. 27, 1895) is in some ways more acceptable than several later ones. All these systems have the weakness of being based exclusively on a small selection of morphological characters, primarily on the shape of the bill and feet. Nothing could be more misleading, for the form of bill or feet is entirely functional and undoubtedly often recently acquired, representing merely a secondary adaptation that is repeated in widely separate groups. It is useful in distinguishing species but has certainly no deeper phylogenetic significance. Non-adaptive morphological characters are far more useful taxonomically. The most important of these in the duck family are: pattern of tarsus (whether scutellate or reticulate in front), a very fundamental character in the family; plumage pattern in both adults and young, the downy young of most of the nine main groups in the family having a very characteristic pattern; presence or absence of a double annual molt; posture, general body proportions, length of neck, and shape of head, all of which show characteristic differences among the nine main groups; characteristics of the internal anatomy, especially the structure and shape of the syrinx and trachea (as Heinroth has repeatedly pointed out[1]). Similarly, biological characters—almost entirely ignored by the currently adopted systems of classification—are of paramount importance to the classifier, for habits and behavior are deeply rooted and are usually the product of very ancient evolution. In the duck family the main points are pair formation, displays, nesting, and feeding habits. To be satisfactory and reliable, any system must be based on the greatest possible number of known characters, and an overvaluation of a few primarily functional characters has led to great confusion in the taxonomy of the Anatidae.

Several branches, for example, the pochard group, the goldeneye-merganser-scoter group, and the stiff-tailed duck group, have developed into divers par excellence, and are structurally rather similar to one another. However, their non-adaptive characters, such as the general proportions of the body, the color pattern of the downy young, the structure of the syrinx, and the courtship performances, are sufficiently different among the three groups to suggest that the three are not at all closely related.

A further instance is that of the so-called geese. In addition to the typical geese of the *Anser-Branta* group, there are a number of

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[1] We refer to his detailed account (O. and M. Heinroth, 1928:226–229). The taxonomic advantage of this structure lies in the fact that its shape is not easily modified by any peculiar adaptations of a given species. It tends to be phylogenetically conservative.

"goose-like" genera such as the Cape Barren Goose (*Cereopsis*), the Pied Goose (*Anseranas*), the Maned Goose (*Chenonetta*), the South American "geese" (*Chloëphaga*), the Egyptian Goose (*Alopochen*), and the group commonly known as sheldrakes ("*Casarca*" and *Tadorna*), all of which are characterized by rather large size and long legs, many by grazing habits. They are the "ungulates" of the duck family. Again the evidence is rather strong that the goose-like features were acquired independently by the several groups. This adaptability poses a problem to the classifier of the duck family which by no means has been solved entirely. However, even though the position of certain species and genera is still uncertain, the study of live specimens and the consideration of previously neglected morphological characters have shed much light on the relationship of the birds included in this family.

This might be an appropriate place to state again our views on the subject of zoological nomenclature. We have always stood for the strict application of the law of priority, but according to the rules and opinions of the International Commission. These provide for corrections in evident cases of misprints, of lapsus calami, and of errors in transcription. There is sometimes a certain difficulty in determining the validity of the evidence for such mistakes, but moderate degrees of common sense and classical scholarship are usually sufficient to enable a zoologist to make up his mind. To retain the original spelling of a name, however wrong it evidently is, constitutes a retrograde solution too easy and too uncritical. It is a great pity that both the A.O.U. and the B.O.U. committees on nomenclature have recently chosen to follow such a course. We are absolutely opposed to it, now as in the past,[2] and consequently we correct all misprints, lapsus calami, and errors in transcription. Also, according to the same rules, the endings of the adjectival species names should agree with the gender of the genus, and Greek endings should not be latinized. Furthermore, we conserve long-used names, unless the necessity for a change is unequivocally established.

We believe in large genera, since it is the function of the generic name to express relationship (as an aid to the memory), not distinctness, which is expressed by the species name. Even Peters, who is certainly not a splitter, recognizes in the family of Anatidae 62 genera for 167 species (an average of 2.7 species per genus), and 42 (70 per cent) of his genera are monotypic. The A.O.U. Check-List goes even further. Such nomenclature comes dangerously close to being mononomial. The modern broadening of the species concept (Mayr, 1942:102–122) necessitates a corresponding adjustment of the genus limits. In the classification here presented we recognize 40 genera for 144 species (3.6 species per genus). It is interesting to find that a number of the vernacular names for the waterfowl—swans, scoters,

[2] See Delacour, 1931, *L'Oiseau*, n. s. 1:438–440.

eiders, mergansers—delimit natural groups more accurately than the generic names currently used by taxonomists. It has been our endeavor to bring the generic nomenclature of the duck family back to an expression of these natural groups. The proponents of generic splitting forget that if morphological difference is acknowledged as an inevitable generic criterion, sooner or later nearly every species will deserve a genus of its own. Generic subdivision carried to extremes not only places an unbearable burden on the memory of the taxonomist, but also completely obliterates the difference between the weak and the really distinct genera. The differences separating *Anser*, *Philacte*, and *Chen; Anas*, *Nettion*, and *Dafila; Aix* and *Dendronessa;* or *Somateria*, *Arctonetta* and *Polysticta*, are certainly very slight compared with the differences separating *Anser*, *Cygnus*, and *Coscoroba;* or *Chloëphaga*, *Alopochen*, and *Tadorna;* or *Anas*, *Malacorhynchus*, *Tachyeres*, and *Stictonetta*. Since no category above the genus can be expressed in the scientific name, the splitter has no way of making a distinction between "weak" and "good" genera. We consider this another strong argument in favor of recognizing only pronounced genera. (Mayr, 1942:280–291.)

A New Classification of the Anatidae

The new classification of the duck family that we propose attempts to do two things: to arrange the species in related groups and in a natural sequence, and to adjust the nomenclature of species and genera to progressive concepts of these categories.

Following the popular classification of this family, the first taxonomists divided the waterfowl into: swans, geese, ducks, and mergansers. As more and more was learned about the anatomy as well as about the habits of members of the family, it was realized that this simple division was unsatisfactory. For example, Linnaeus included in the duck genus *Anas* such widely divergent species as the river ducks of the mallard and teal type, the diving ducks of the scaup-pochard group ("*Nyroca*" = *Aythya*), the diving ducks of the goldeneye-scoter-eider group (Mergini), the tree ducks (*Dendrocygna*), and the sheldrakes (*Tadorna*). Although subsequent classifiers recognized some of these subdivisions, they were guided in their reclassification mainly by the shape of the bill or by the presence or absence of the diving habit.

All the ducks, geese, and swans, including even the most aberrant species, are so much alike in their basic structure and habits that there can be no doubt that those modern authors are right who include all waterfowl in a single family, the Anatidae. Within this family a number of groups of genera can be recognized, but they are clearly arranged in two main groups, which we admit as two subfamilies:

(1) Anserinae. This subfamily includes the swans, geese, and the whistling ducks ("tree" ducks). The attributes of the group are a "goose-like" posture and body shape (with a long neck); a tarsus reticulated in front; a single annual molt; absence of sexual dimorphism in plumage, voice, and structure of the syrinx. Displays are simple and are similar in the two sexes.

(2) Anatinae. This subfamily includes the rest of the Anatidae. The attributes of the group are a tarsus that is scutellated in front (with a few exceptions); a double annual molt; sexual dimorphism in plumage (frequent), in voice and structure of syrinx (usual). Displays are usually elaborate and different in the two sexes.

Within each subfamily further subdivisions are recognizable. We use the term tribes (with the ending *-ini*) for such groups of genera, following a custom that is widespread in entomology. The reasons for the recognition as well as for the delimitation of these tribes will be found in the following discussion. The phylogenetic relationships within the duck family are diagrammed in Figure 1.

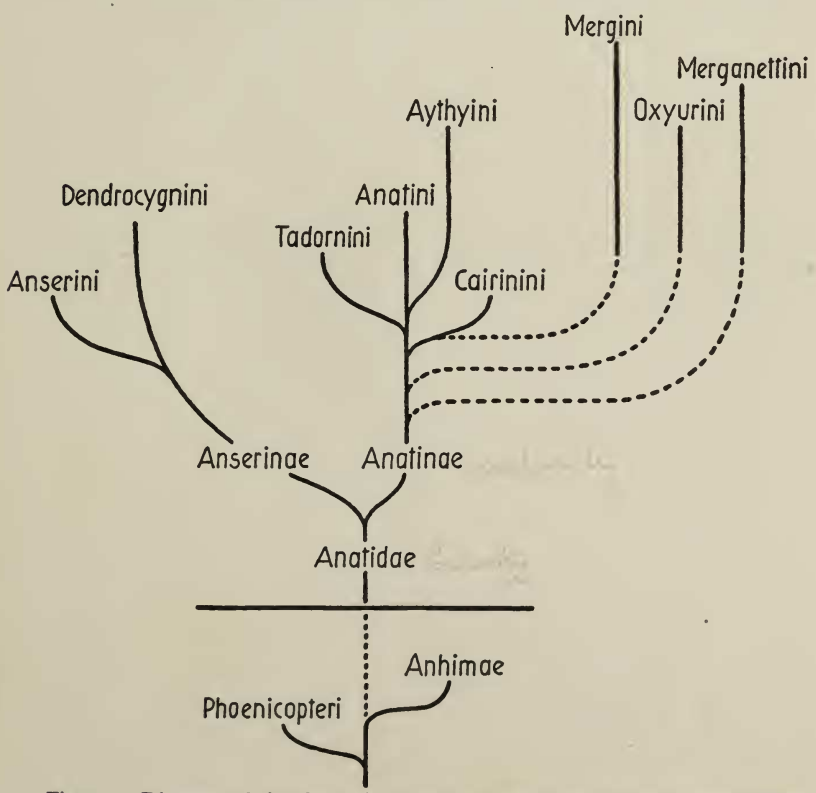


Figure 1. Diagram of the theoretical relationships of the subfamilies and tribes of the Anatidae.

I Subfamily Anserinae

1. tribe anserini. swans and geese

The birds commonly known as swans and geese agree so closely in structure, in pattern of downy plumage, in general behavior and courtship, and in living and nesting habits, that they cannot be separated as two distinct tribes. Swans differ from geese only in their larger size, shorter legs, longer necks, and greater number of vertebrae; none of these characters is taxonomically important, not even the number of vertebrae, since this varies considerably from species to species.

The Anserini differ sharply from most of the other waterfowl. The two sexes are always similar in plumage, and nearly so in voice, the voice of the female being merely a little higher pitched. They never have any metallic colors, and the downy young never have a strongly marked pattern. The nuptial display and mating antics are all simple and vary little among the species; the only courtship consists of stretching the neck and of "dipping." They apparently pair for life, and both male and female always participate in the care of the young. Usually it is the female which incubates, while the male guards the nest. In the exceptional case of the Black Swan (*"Chenopis" atratus*), the male shares to some extent the duty of incubation. Sexual maturity is not attained until the second or third year. Swans and geese have only one annual molt and consequently have no eclipse plumage. They nest on the ground; a few species nest occasionally on ledges or in old nests. Their food is mostly vegetable, obtained by grazing and dipping. Their syrinx is symmetrical and has no bulla.

We consider all swans as congeneric, the fact that some have black in the plumage being of little importance. The most primitive swans are arranged in two pairs of forms: *bewicki* (Old World) and *columbianus* (New World); *cygnus* (Old World) and *buccinator* (New World). As Hartert has already suggested, these are best considered two Holarctic species (*C. columbianus* and *C. cygnus*). The four forms are alike in behavior patterns. Each of the three other species of the genus stands rather alone, although the Mute Swan (*C. olor*) and the Australian Black Swan (*C. atratus*) show certain similarities. The threat behavior of lifting the wings, which is so typical of the Mute Swan and occurs in a less pronounced way in the Black Swan, is absent in the Black-necked Swan (*C. melanocoryphus*) as well as in the four primitive forms.

Pair formation, which occurs in the fall in all temperate-zone swans, takes place without elaborate displays. According to Heinroth (1911), birds that are in the process of pairing swim in close proximity,

Figure 2. Canada Goose (*Branta canadensis*) with young.

Figure 3. Hawaiian Goose (*Branta sandwicensis*).

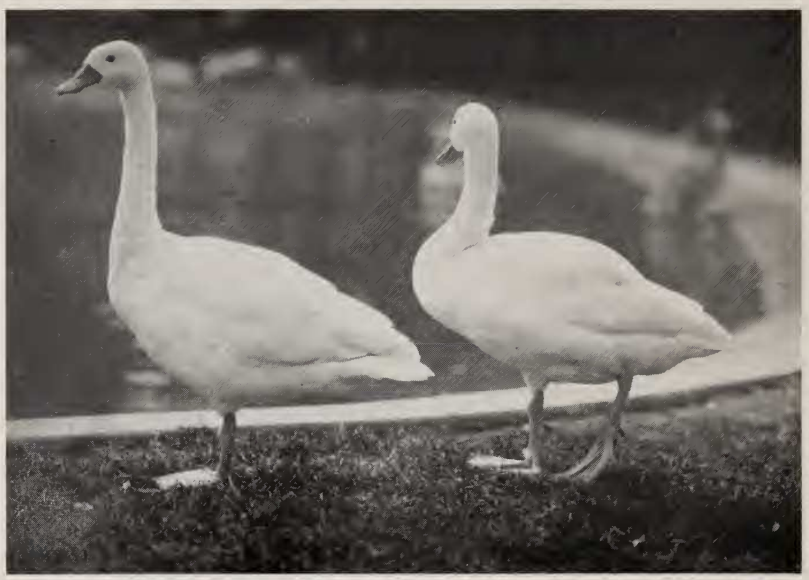


Figure 4. *Coscoroba coscoroba.* Compare with Whistling Duck, Figure 5.

Figure 5. White-faced Whistling Duck (*Dendrocygna viduata*).

Figure 6. Plumed Whistling Duck (*Dendrocygna eytoni*). Compare body posture with that of Canada Goose in Figure 2.

Figure 7. Cape Barren Goose (*Cereopsis novae-hollandiae*) with young. Compare posture of adults with that of Magellan Goose in Figure 8 and pattern of young with young in Figure 9.

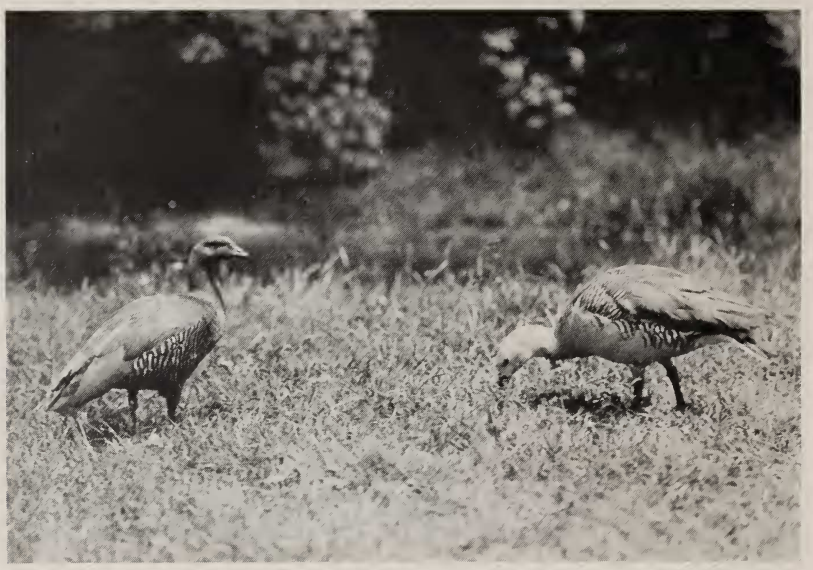


Figure 8. Magellan Goose (*Chloëphaga picta*) walking and feeding. Male on right.

Figure 9. Ashy-headed Goose (*Chloëphaga poliocephala*), pair with young.

Figure 10. Orinoco Goose (*Neochen jubatus*) with young. Bold pattern of downy young typical for tribe Tadornini.

Figure 11. Pied Goose (*Anseranas semipalmata*).

Figure 12. African Spur-winged Goose (*Plectropterus gambensis*).

Figure 13. Comb Duck (*Sarkidiornis melanotos*). Note thick short neck, horizontal body posture, and long tail.

press the plumage close to the body, and hold the neck in a peculiar position, the head appearing thickened. Swans, geese, and whistling ducks (tree ducks) have essentially the same precopulatory display: both birds of a pair repeatedly dip the whole head and neck until finally the female flattens herself out on the water and sinks deeper with the neck half extended. But there are a number of variations; for example, in swans male and female frequently face each other and half rise out of the water, breast to breast. All swans, except the Mute Swan, have been observed diving, although rarely. They seem to be the only Anatidae which have the habit of taking their downy young on the back when the young are tired or cold. This is the usual practice with Mute and Black-necked Swans. It is exceptional in the other species.

Amongst the geese, there is no ground for retaining the genera *Chen*, *Cygnopsis*, *Eulabeia*, and *Philacte*, all the species referred to them being members of the genus *Anser*. All have more or less strong serrations on the sides of the bill. *Branta* is characterized by a more elaborate plumage pattern, a longer and thinner neck, and smaller and smoother bill (Figure 2). The Hawaiian Goose ("*Nesochen*") certainly belongs in this genus (Figure 3). Hybrids from crosses between species of *Anser* are usually fertile, and so are those between species of *Branta*, but hybrids from crosses between the two genera are sterile.

The Russian workers (for references and summary see Ernst Hartert and F. Steinbacher, 1936, "Die Vögel der paläarktischen Fauna", Erg.Bd., Heft 5:433–434) have shown that *brachyrhynchus* and *neglectus* are races of *fabalis*. The extensive breeding ranges of *Anser erythropus* (inland) and *A. albifrons* (coastal) run parallel along the north of Europe and Asia. No overlap of the ranges of the two species is known, and it has therefore been suggested (Witherby *et al.*, 1939) that the two forms be considered subspecies of *erythropus*. Further work may show that this view is correct.

The most characteristic feature of the geese is their closely knit family life. The family migrates as a unit, and the young apparently remain with their parents until the beginning of the new breeding season.

The "triumph ceremony," which is characteristic of the geese, has been described as follows: "After driving off intruder all geese behave similarly; gander hurries back to mate with special 'triumph-note' . . . in which she joins, uttered with neck stretched out and head close to ground. Even downy young take part, assuming same attitudes as parents" (Witherby *et al.*, 1939:182, *after Heinroth*). The same "triumph ceremony" is an important part of the pair-formation display. The courting gander drives away weaker birds and then returns to the chosen goose with the "triumph note." At first, she may not pay much attention to his behavior, but if she

answers his call and joins in the display, the pair formation may be considered completed. The gander swims in a peculiarly proud, erect position in the water during this courtship period and may indulge in "dipping displays" even before pair formation. The pre-copulatory display is the same as in the swans.

Geese are highly social, as are most grazing animals. Manifestations of social rank seem to be absent in the wild, but develop in confinement when the source of food is localized. Geese mature in the second year, and pair formation takes place in the second winter. The habits of the various species of *Branta* seem to be essentially the same as those of *Anser*, except that the smaller species feed to a greater extent on water plants.

The very peculiar *Coscoroba coscoroba*, from South America, occupies a special place. It reminds one of a swan by its white color and some of its habits. Particularly, it raises its wings in anger as the Mute and the Black Swan do. At the same time, its voice (a not very loud, trumpeting *cos-córoba*) and its display are entirely peculiar. In some other features (in shape of head, for example) it resembles the whistling ducks, it has their long legs and large feet, their comparatively rounded wings (Figures 4 and 5). The downy young, extremely rare in collections, is, like a cygnet, whitish-gray, but it shows in darker gray, distinctly if weakly, the very special markings of the downy whistling duck, notably the light band across the nape. As in swans, the syrinx is without a bulla, even in the male.

Coscoroba, in fact, seems to be an intermediate, linking the swan-goose group to the whistling ducks, and on that account is of very great interest. On the basis of the scanty information available, the genus *Coscoroba* could be placed in either group. A thorough study of its anatomical features, of its pair formation, and of the participation of the male in incubation and raising of the young is needed before the species can be classified with confidence.

2. TRIBE DENDROCYGNINI. WHISTLING DUCKS ("TREE DUCKS")

Whistling ducks are among the least known of all the ducks. There is not a single good life history of any of the species, nor is there an anatomical comparison of the tribe with other Anserinae. The tribe is composed of a single genus (*Dendrocygna*) with eight species. Whistling ducks have no close relatives except *Coscoroba*. Their high-pitched, squeaking voice and a number of their habits are peculiar to the tribe.

They have a number of features in common with the other Anserinae. Both sexes take care of the young. The male shares (?always) in the duties of incubation, as in the Black Swan; in fact, in *viduata* and *bicolor* the male seems to have the greater share. The two sexes are alike in coloration and similar in voice; they seem to

pair for life. There is no metallic color in the plumage. Whistling ducks resemble geese in postures (Figure 6) and display. Their food consists mostly of vegetable material and is obtained by grazing, dipping, or diving. They are expert divers and gather much of their food under water. They nest usually on the ground, in reeds or tall grass, where they build an elaborate nest, well concealed by bent-over stalks; they nest occasionally in holes in trees or in abandoned nests of other birds. Their eggs are white and rather round. The pre- and post-copulatory displays are the same as those of swans and geese, different from those of the Anatinae: male and female face each other, lift the breast out of the water, and slightly raise their wings.

Their syrinx has symmetrical bullae, slightly larger in the male than in the female. The plumage patterns of adults and downy young are peculiar, different from those of all other Anatidae (excepting only *Coscoroba* as noted above). The fully adult plumage is attained the first year. The species of whistling ducks show very little geographical variation.

In spite of their common name these ducks seldom perch in trees. Some species never do, while others perch only occasionally—not nearly so regularly as the members of the tribe Cairinini. Hence "whistling ducks" is a much more appropriate name for this group than "tree ducks."

The eight species of *Dendrocygna* can be divided into three groups: a primitive group (perhaps only one superspecies) consisting of *arborea* (West Indies) and *guttata* (East Indies); secondly the somewhat isolated species *autumnalis* (America); and finally a group of five closely related species, *javanica* (southeast Asia, Malaysia), the superspecies *bicolor* (America, Africa, India) and *arcuata* (Malaysia, Papua, Australia), *eytoni* (Australia), and the specialized *viduata* (America, Africa, Madagascar).

II Subfamily Anatinae

1. tribe tadornini. sheldrakes

The sheldrakes, a name under which we include the related genera *Chloëphaga*, *Cyanochen*, *Neochen*, *Alopochen*, "*Casarca*," and *Tadorna*, form a group of ducks which are not far from the river ducks. The resemblance to the geese, which has led to names like Egyptian Goose, Orinoco Goose, and Blue-winged Goose, is entirely superficial. The South American Crested Duck (*Lophonetta*) is related to the sheldrakes, as are probably also the primitive Australian Cape Barren Goose (*Cereopsis*) and the South American steamer ducks (*Tachyeres*).

Members of this tribe are characterized as follows: bill comparatively short and thick; legs long; neck short; coloration in the two

sexes either alike or different, but bright in both; voices of male and female very different; a spur-like bony knob on the bend of the wing (metacarpal joint); a bold color pattern of the downy young (black and white or grayish-brown and white); a white nest-down in many species; wings adorned (except in *Cereopsis*) with a broad metallic speculum, which is formed by the secondaries or greater wing coverts; lesser and median wing coverts of a uniform snowy white (except in *Cereopsis* and *Cyanochen*, where they are light grayish-blue, in *Neochen*, where they are purplish-black, and in *Lophonetta specularioides*, where they are gray). Sheldrakes are very quarrelsome; each pair keeps apart from other individuals of the species.

Females indulge in special "incitement displays" which are important in pair formation. In the Ruddy Sheldrake (*Tadorna* ["*Casarca*"] *ferruginea*) in which this display is particularly well developed, it has been described as follows: "On approach of intruder female makes kind of feigned attack, with neck extended and head close to ground, constantly uttering anger-note, and if it does not withdraw she returns to male, running frantically round him . . . . till he attacks the stranger and if possible drives it off. Male appears to have no courtship, but female takes initiative in attaching herself to a male and inciting him to attack others . . . . Females not yet definitely paired may incite different males against one another, apparently preferring strongest and most bellicose" (Witherby *et al.*, 1939:228, *after Heinroth*). These agitation displays occur in rudimentary form also in the mallard and other river ducks.

The eggs are smooth, not rough as in the geese, and only the females incubate. The males, however, guard the nest from a distance. The Tadornini apparently pair for life, but accurate observations on this point are not available. Members of the genus *Tadorna* nest usually in holes in the ground except *T. radjah*, which nests in tree holes. Accurate records of the nesting habits of *Cyanochen* or of *Lophonetta* in the wild are lacking. *Chloëphaga* and *Cereopsis* nest on the ground. Sexual maturity and the pugnacity connected with it are usually reached at the age of two years. Adults of the tribe dive only when wounded and before coition (*Tadorna*). The pre-copulatory display of *T. tadorna* does not consist of head and neck dipping as in geese, but of a simultaneous dive by the two sexes during which the male mounts the female. In *Alopochen* and *Chloëphaga* copulation may occur in shallow water or even on land. The food of most species consists of grass and water plants (eelgrass, kelp), but a few forms, particularly *T. tadorna*, feed also on mollusks, shrimp, and other water animals.

The grazing habits of the five species of *Chloëphaga* are correlated with a *Branta*-like bill, as in *Cyanochen* and *Neochen*. The color pattern of the downy young, the wing pattern (with metallic speculum) of the adults, the asymmetrical development of the bulla ossea

of the syrinx, the sexual dimorphism in voice, the scutellation of the tarsus, and many other features prove the relationship of *Chloëphaga* with the sheldrakes.

The species of this tribe form a graded series from long-legged birds with a narrow bill, as in *Chloëphaga*, to birds which have shorter tarsi and a longer, broader bill with more distinct lamellae, as in *Tadorna*. The gap between the sheldrake tribe and the river ducks seems to be bridged morphologically by such intermediate forms as *Lophonetta specularioides* on one side and *Anas specularis* and *A. acuta* on the other. However, sheldrakes have larger tails than river ducks, and their legs are longer and placed more forward; they also differ strikingly in their habits. It is therefore justifiable to keep them in a separate tribe.

The Cape Barren Goose (*Cereopsis novae-hollandiae*) is a peculiar bird, quite different from typical sheldrakes in many respects, including skull, bill, and color pattern of the adult. The tarsus is reticulate and the syrinx without bullae, both characters indicating a primitive condition. On the other hand, the color pattern of the downy young, the general proportions of the birds, their posture (Figures 7 and 8), as well as their quarrelsome temper, indicate relationship with *Chloëphaga*, as Heinroth (1911) pointed out many years ago. The real place of this primitive genus in the duck family is still somewhat uncertain. The sexes are alike in plumage. The voice of the male is loud and trumpeting, that of the female a low grunt. The bill is short and thick, covered for the greater part by a yellow cere. The nest is placed on the ground.

All the South American "geese" of the genus *Chloëphaga* (Figures 8 and 9) are nearly alike in shape and habits. The males have a high-pitched whistle, the females a harsh quack, very similar among all species. Their breeding display is interesting, distinctly like that of the typical ducks. The male stands erect, throws the breast forward, the neck backward, and calls, while slightly lifting the wings; the female quacks with lowered head and a vertical movement of the neck. In the Andean species (*C. melanoptera*), the display is more elaborate, and both sexes puff out their feathers; the voice is softer. There is an eclipse plumage in *C. poliocephala*, grayer and less bright than the nuptial, between the postnuptial and the late fall molts, affecting both sexes. The sexes are similar in plumage in three species (*rubidiceps*, *poliocephala*, *melanoptera*), different in the other two (*hybrida* and *picta*[3]). The downy young of the various species (Figure 9) are similar to one another in pattern, but some have very dark gray marking (*poliocephala* and *melanoptera*); others are paler and browner (*picta* and *rubidiceps*); while in *hybrida* they are ex-

[3] We include in *picta* both *dispar* and *leucoptera*. For the use of the name *picta* instead of *dispar* or *leucoptera*, see Hellmayr, 1932, *Field Mus. Nat. Hist. Zool. Series*, 19:319.

tremely pale. The metallic speculum in *Chloëphaga* is formed by the greater wing coverts, while the secondaries are white.

The Abyssinian Blue-winged Goose (*Cyanochen cyanopterus*) could almost be considered congeneric with *Chloëphaga*, differing only in its slightly flatter bill, its more graduated tail, its blue wing coverts, its metallic green secondaries, and its alarm display. The voice in both sexes resembles that of *Chloëphaga melanoptera*, but is still softer. As in *C. melanoptera*, the face of the downy young shows during the first days after hatching a distinct golden tinge, a feature found only in these two species of the tribe. When alarmed, *cyanopterus* puffs out its shoulder feathers and rests its neck among them. Otherwise, it has the same general aspect, habits, and display as the species of *Chloëphaga*.

The Egyptian (*Alopochen*) and Orinoco (*Neochen*) Geese are related, the bill in *Neochen* being slightly, and in *Alopochen* decidedly, flatter and broader than in *Cyanochen* and *Chloëphaga*. The male Orinoco whistles, whereas the male Egyptian emits a husky breathing sound. In addition to this difference in bill and voice, the plumage pattern of adults and the coloration of the downy young are different, as well as the display postures. It may, therefore, be justifiable to recognize the genus *Neochen*. (The Orinoco Goose and downy young are shown in Figure 10.) Both females have harsh quacking voices. Their displays, although special in each case and very elaborate in *Neochen*, recall those of *Chloëphaga*, except that the wings are opened a little more. The nest is placed by preference—particularly by the Orinoco Goose—in a hollow tree or in a hole in the ground, but always in some sheltered site. The sexes in both species are alike.

The typical sheldrakes are usually placed in two genera, *Tadorna* and *Casarca*. The two type species, *tadorna* and *ferruginea*, the European representatives of these groups, are indeed strikingly dissimilar. However, they are connected by a chain of intermediates. The Australo-Papuan species *radjah*, for example, has the body shape, syrinx, and downy plumage of "*Casarca*," the whistling voice of "*Tadorna*" in the male, a bill and plumage pattern intermediate between the two "genera," and it nests in trees, which neither typical *Tadorna* nor typical "*Casarca*" do. The Australian *tadornoides* approaches *Tadorna* in color pattern. It is best for this reason to group all of the typical sheldrakes in a single genus, *Tadorna*, in which we also include "*Pseudotadorna*" *cristata*. This probably extinct Korean form resembles *Lophonetta* in having a slight crest and a rather graduated tail, but in every other respect it agrees perfectly with the other species included in *Tadorna*.

The species of *Tadorna* have a flatter bill (slightly curved, with distinct lamellae) and shorter tarsi than the goose-like species described above. Both sexes in the four species formerly separated

as "*Casarca*" (*ferruginea, cana, tadornoides, variegata*) have a loud voice, which they use very often in duets; that of the female is very different from the male's—harsh and quacking. The display resembles that of *Chloëphaga* and particularly that of *Alopochen*. The male moves his erect head backward and forward; the female stretches her neck and keeps her head low as in most other Tadornini. They nest in holes and burrows. An interesting fact is that the juvenal plumage of both sexes resembles that of the adult male. It is always different from that of the female although not conspicuously so, except in one species (*variegata*), in which the female has a distinct, blackish, eclipse plumage.

The Common Sheldrake (*tadorna*) differs from the other species primarily in the whistling voice of the male and the showy black, red, and white plumage. It is also less quarrelsome and more gregarious. If associated with them in captivity, *T. radjah* pairs with *T. ferruginea* (with which it produces fertile hybrids), but completely ignores *tadorna*.

The South American *Lophonetta specularioides* resembles the members of the genus *Anas* in its plumage pattern. But in its quarrelsome, solitary habits, its display and general behavior, and the pattern of the downy young, it is undoubtedly a member of the sheldrake tribe. It provides an obvious link between the tribes Tadornini and Anatini.

The large, robust, and plain-colored steamer ducks (*Tachyeres*) of the austral coasts of South America are difficult to place. We have long observed them at Clères. They have almost no display, and their habits and voice seem to be very simple and primitive. They are great divers and superficially resemble the eiders to which, however, they are obviously not related. They are exceedingly quarrelsome and combative, as are many genera of Tadornini. The color pattern of the downy young is characterized by a broad white stripe (interrupted in *pteneres*) along the side of the head, rather similar to the pattern of the young in *Chloëphaga*. It is possible that the steamer ducks are diving species evolved from the *Chloëphaga* group, and we therefore tentatively associate them with the Tadornini. The male steamer duck helps the female in raising the young, and there is some evidence that steamer ducks pair for life. This habit would also favor classification with the Tadornini. The male has an asymmetrical bulla ossea of the syrinx, like that found in the Tadornini, Anatini, and Cairinini. The secondaries are white, as in *Chloëphaga*.

As Murphy has convincingly demonstrated (1936, "Oceanic Birds of South America," pp. 951–972), there are three species of steamer ducks, a flying species (*patachonicus*) and two flightless ones (*pteneres* and *brachypterus*).

2. TRIBE ANATINI. RIVER DUCKS

The river ducks, also called surface-feeding ducks, occupy a central position among the Anatinae, between the sheldrake tribe of mostly grazing species and the diving tribe of pochards. We recognize about 36 species of typical river ducks and 4 aberrant species which we classify with them only tentatively.

River ducks differ from the sheldrake tribe most noticeably in their smaller, more pointed tail; the legs are shorter and are placed farther back on the body, which is the reason for their waddling walk. They go to the shore or ice to rest more frequently than the pochards or sea ducks do. The wings are long and pointed and are beaten less rapidly than among the pochards and sea ducks. The hallux is not lobed. The syrinx of the male has an asymmetrical bulla (always on the left side), which is evenly ossified. The sexual dimorphism of the syrinx is correlated with a pronounced difference in voice between the sexes, the voice of the female usually being louder.

All river ducks have two molts each year. In about half the species the plumages of the two sexes are dull colored and very similar; in a few species (e.g. Chilöe Widgeon, *Anas sibilatrix*) both male and female are brightly colored. There is strong sexual dimorphism in the brighter forms of the northern hemisphere and in some southern forms; in these species the nuptial plumage of the drakes is very different from the eclipse plumage, which resembles that of their females. In the dull-colored species (and in the species in which both sexes are bright), there is very little difference between the nuptial and eclipse plumage (Falla and Stead, 1938). The female and eclipse plumages of the brightly colored species have a hormonal basis. Castrated males and females of such species wear the nuptial plumage of the drake throughout the year. All species have an iridescent metallic speculum. The downy young of all species of the genus *Anas* are very much alike (similar to those of the mallard). They are usually yellow and brown with a dark line across the eye.

Most river ducks live on fresh water, but a few species nest on the seashore; some are found on the ocean during migration. They get most of their food in shallow water, securing it from the surface; or from mud with quick dabbling motions of the mandibles; or, where water is slightly deeper, by "up-ending" (tipping) with head and front part of body submerged and tail in air. Young dive fairly freely, but adults only exceptionally or if wounded. *Anas sparsa* alone among typical river ducks is reported to dive regularly. Only a few species perch in trees and nest in holes. All river ducks breed when one year old. They have larger clutches than the pochards, but the eggs are smaller.

The typical river ducks consist of 14 groups, characterized by minor morphological and biological peculiarities, but all closely related and more or less connected by intermediates. One must either

recognize 14 separate genera or unite all these species in the single genus *Anas*. The latter arrangement, originally proposed by Hartert, has largely been adopted by Phillips, Peters, and Witherby, but, curiously enough, all of these authors have kept the shovellers in the separate genus *Spatula*. The extremely close relationship of the four species of shovellers with the three "teal" of the blue-winged group (*querquedula*, *discors*, *cyanoptera*) is, however, evident and has been emphasized by many authors. All these species have an almost identical color pattern of the wing. The peculiar courtship habits, the feeding methods, and sometimes the voices are similar among the species and somewhat different from those of the other river ducks. The only difference between "*Querquedula*" and "*Spatula*" is the larger body and bill in the shovellers. Furthermore, there is good evidence that the shovellers are not even a natural, monophyletic group. In two pairs of species, the South American Shoveller (*platalea*) and the Cinnamon Teal (*cyanoptera*) on one side, and the Australian-New Zealand Shoveller (*rhynchotis*) and the Blue-winged Teal (*discors*) on the other, the "teal" of each pair agrees in plumage color with the "shoveller" to such a surprising degree that the closest relationship must be assumed. This suggests that the shoveller group is polyphyletic, owing its origin to the repeated development of large-sized and large-billed species from the original blue-winged duck stock. Again, as in so many other cases in avian taxonomy, the shape of the bill has been a very misleading character. In addition to *Spatula*, Peters also maintains the genera *Mareca* (for the widgeons) and *Chaulelasmus* (for the gadwalls), but this action is, in our opinion, not consistent with the lumping of the other groups.

The display among the river ducks follows a common pattern, but it shows every degree of elaboration from a few simple performances to a complicated series of displays. These more or less elaborate displays, which are accompanied by distinctive calls, provide excellent clues to the relationships among the various species, even better ones than color patterns and morphological features. Pursuit flight is common with most species.

The most elaborate display is that of the Mallard (*Anas platyrhynchos*). It may be described in detail, to form a basis of comparison with other species. It consists of a series of postures, the principal of which are: (1) Swimming around the female, or sitting on the water with other drakes, with head sunk, the feathers puffed out, and neck resting on the back; tail shaken and raised and head shaken repeatedly. (2) Quick "throw-up" of head and tail, at once followed by No. 3. (3) Neck stretched out over the water, the bird swimming about swiftly in various directions. (4) Following posture No. 1, the bill is suddenly lowered and dipped in water; the bird then stands up and rapidly passes its bill up his breast, producing a jerk which throws up a small jet of water as bill is withdrawn. A whistle is

emitted during this display. (5) The drake swims around with neck raised and head slightly turned, as the female displays at his side. The female follows the male, quacking, with head lowered and repeatedly moved sidewise away from the drake as if to defy others to approach her mate. She also assumes posture No. 3 of the males. In all typical Anatini, the precopulation display in both sexes consists of a bobbing up and down of the head, the bill touching the water at its lower course and always remaining nearly horizontal. Finally, the female flattens herself, extends her neck, and is mounted by the male. In species most nearly related, these postures are reproduced with only minor changes or omissions. In other groups, some or most of the postures are lacking, while in still others the display is very simple and primitive or considerably modified (blue-winged ducks).

Making use of all these characteristics, we arrange the 36 species of river ducks of the genus *Anas* in a number of groups which were given subgeneric rank in an earlier publication (Delacour, 1936). In order to avoid complicating the nomenclature, we refrain from listing subgenera here. This does not mean, however, that we do not fully recognize the validity of these subdivisions of the genus *Anas*.

Group 1. The Bronze-winged Duck

The Bronze-winged Duck (*Anas specularis*) of South America, the only member of this group, remains poorly known. We have never observed it in life. Although in its plumage it resembles the Crested Duck (*Lophonetta specularioides*) of the same region, it seems closer to the river ducks in its general proportions. So far nothing is known of the habits, voice, and courtship display of this species. Recent observers report that it is a sociable bird, gathering in flocks. Its present place in our system is tentative.

Group 2. Salvadori's Duck

Salvadori's Duck (*"Salvadorina" waigiuensis*), from the mountains of New Guinea, is very close to the birds of the following group in its proportions and color pattern. Its reputed adaptation to life in rapid mountain streams has been greatly exaggerated, and it shows no resemblance to the Torrent Duck (*Merganetta*); the tail feathers are hardly stiffer than those of other ducks. The bill is fairly broad, and the head is entirely black. Otherwise the species agrees very well with birds of Group 3. The habits are those of typical river ducks (Mayr and Rand, 1937, *Bull. Amer. Mus. Nat. Hist.*, 73:9–12).

Group 3. "Tropical Pintails"

A group, inhabiting tropical and subtropical countries, which consists of species that are very near the pintails of Group 4 though less

specialized, can be called the "tropical pintails." The tail is pointed but shorter; the male's voice is lower and less melodious; the display resembles that of the pintails of Group 4 but is simpler, lacking the more elaborate postures to a varying degree according to species. Male and female are alike in all species, and the eclipse plumage resembles the nuptial. The following six species belong to the group: *angustirostris*, *capensis*, *punctata*, *versicolor*, *erythrorhyncha*, and *bahamensis* (with subspecies *galapagensis*). They all have a comparatively large head, dark above, pale below; a thin and rather long neck; a narrow and fairly long bill, which is depressed, curved, and always brightly colored. All have a speculum, bronze-green with light-brown borders, except in *angustirostris*, where it is whitish gray. The latter is a pale species, but its shape and general plumage pattern indicate clearly its relationship to the others, particularly to *capensis*. The males of *A. versicolor* and of *A. punctata* are practically voiceless, and the male of *versicolor* has, according to Heinroth (1911), a peculiar enlargement of the middle of the trachea.

Group 4. Pintails

The Common Pintail (*Anas acuta*) is very similar to the mallard in general habits and display. In courtship posture No. 2, the tail is raised vertically; posture No. 3 is usually omitted. The call of the drake is a soft *klyck*, very much like that of the green-winged teals (Group 5). Like the mallard it emits a whistle during Posture 4 of the courtship. Eaton's Pintail (*eatoni*) is colored like the eclipse plumage of *acuta* and is obviously conspecific with it, differing mostly in its smaller size. The close relationship of *acuta* with the mallard is indicated by the frequent crossing of the two species and by the almost unlimited fertility of the hybrids. Pintails seem to indulge in "up-ending" more than any other duck, the greater frequency of this habit being undoubtedly correlated with the longer neck of the species. The South American Brown Pintail (*A. georgica spinicauda*) has a yellow bill and throughout the year a spotted fulvous-brown dress in both sexes. The South Georgian Pintail (*A. g. georgica*) is very similar but much smaller and slightly darker. Voice and display are those of *acuta*.

Group 5. Green-winged Teals

The Green-winged Teal (*Anas crecca*) has the same display as the mallard, and its voice, a soft *klyck*, is emitted during Postures 2 and 4 of the courtship. It is represented in South America by the Yellow-billed Teal (*A. flavirostris*) which resembles in plumage the South American Brown Pintail (Group 4). The two forms, together with *A. undulata* (Group 9), differ from their brightly colored northern representatives (*A. crecca*, *acuta*, and *platyrhynchos*) in a remarkably parallel manner.

Group 6. Baikal Teal

The color pattern (Frontispiece) of the Baikal Teal (*Anas formosa*) indicates that it is related to *crecca*. However, voice and display are entirely different and necessitate its separation in a special group.

Group 7. Falcated Teal

The Falcated Teal (*Anas falcata*) of northeastern Asia also stands rather alone. It is perhaps more closely related to the Baikal Teal than to any other group. Its voice, a triple whistle of the pitch of *crecca*, is given without special display. Head and neck are pressed close to the body, and the remarkable sickle feathers of the male are, curiously enough, never displayed. This species seems to be also related to the Gadwall (*A. strepera*), which it approaches in several ways and whose company it seeks in captivity.

Group 8. Austral Teals

A group standing near the mallards is composed of teals from the South Pacific and the Indian Ocean. The relationship of the two groups is shown in a general similarity in shape and in color pattern. Both include some forms with green-headed, bright males, having a distinct eclipse plumage, and some that are dull-colored. The display of the Austral teals is that of the mallards minus the elaborate Postures 3 and 4. They all have the same wing pattern, with a brilliant dark green and white speculum. It is a perching group, often nesting in trees. It is composed of two species with a marked sexual dimorphism: "*Nesonetta*" *aucklandica*[4] (including *Anas chlorotis* as a subspecies) and *castanea;* and two that have a dull brown plumage: *gibberifrons* (including *albogularis* and several other subspecies) and the small erythristic *bernieri*, a rare bird of Madagascar.

S. D. Ripley (1942, *Auk*, 59:90–99) has recently studied *gibberifrons* and concluded that it was conspecific with *castanea*. It is obvious that both forms are very closely related; but it seems that both often breed at the same locality, and we therefore prefer to consider *castanea* a full species. Hybrids reared in captivity are intermediate and completely fertile.

Group 9. Mallards

The mallard group is composed of the well-known northern bird, with a brilliant nuptial and inconspicuous eclipse plumage, and of many other species spread over most of the world except South America. These other species have a dull brown plumage practically the same in the two sexes and in the two annual plumages. The entire group could almost be considered a single superspecies. It is only in North America and East Asia that the breeding ranges of two species of this group overlap. It appears that this overlapping is of recent date and perhaps brought about by human agency. In general behavior, display, and voice, the mallards are alike. It is

[4] We follow Stead (1938, *Trans. Proc. Roy. Soc. New Zealand*, 68:100–101) in placing *Xenonetta nesiotis* Fleming, 1935, in synonymy here.

however, possible to distinguish several groups among them according to their plumage pattern and general proportions, and we find it expedient to accord specific status to each of these groups.

The Hawaiian Duck, Laysan Teal, and Marianas Mallard (*wyvilliana*, *laysanensis*, and *oustaleti*) are small and have lost in their isolation many of the characteristics of the mallard. Still, they are certainly nothing but dull-colored editions of the Common Mallard (*platyrhynchos*) and therefore conspecific with it; all have the same speculum as the Common Mallard. The East Asiatic-Pacific group, which includes *poecilorhyncha*, *superciliosa*, and *luzonica*, as well as other less distinct forms, also constitutes a single species, all the forms being very similar in plumage pattern and shape. The Madagascan Meller's Duck (*melleri*) stands alone, as does the African Yellow-billed Duck (*undulata*); the latter reminds one of the South American Brown Pintail (*A. georgica spinicauda*) and of the Yellow-billed Teal (*A. flavirostris*) by the colors of its bill and plumage, as noted above. The North and Central American group can also be considered as forming one species (*fulvigula*); it seems obvious that the Mexican and Black Ducks (*diazi* and *rubripes*) are only subspecifically distinct from the Dusky Duck (*fulvigula*).

Group 10. African Black Duck

The African Black Duck (*Anas sparsa*), a forest species, stands quite alone in its behavior and habits. It is a quarrelsome species leading a solitary life. Its display is different from that of the other groups and is simpler; its voice is peculiar. This species is probably less closely related to the mallards than is commonly supposed; it requires further study.

Group 11. Gadwall

The display of the Gadwall (*Anas strepera*) is similar to that of the Mallard but is simpler. Posture 4 is usually absent, and instead, a grunting call is uttered without special body movements except that the head is raised. The display performance is more casual and the voice of the female much less loud than in Groups 2, 3, and 7.

Group 12. Widgeons

The three species of widgeons form quite a special group, not closely related to any other. Their display, although it suggests certain parts of that of the mallards, is peculiar. It consists mostly of a lifting of the long scapulars and the primaries accompanied by loud whistling and vertical movement of the head. It is interesting to note that the South American species, *sibilatrix*, in which the two sexes are nearly similar and both brightly colored, has the most elaborate postures. In the European Widgeon (*penelope*) and the American Widgeon (*americana*), which are very closely related, this display occurs in a more rudimentary form. However, the American species lacks the loud whistle, produced before and during the breeding

season, which the European species shares with *sibilatrix*. It seems that in *sibilatrix* the drake helps the female take care of the young, and similar cases have been reported in *americana* and *penelope*, although it does not appear to be the rule with them. This trait is apparently unusual for the genus *Anas*, but parental care of many species of river ducks has been studied insufficiently. The somewhat isolated position of the widgeon is also indicated by the color of the young (which are less yellow than the others) and the apparent sterility of hybrids with other species of *Anas*, except *strepera* (Group 11). The pair among widgeons is a more closely knit unit than in other groups, and although pursuit flight occurs, it is infrequent.

Group 13. Blue-winged Ducks

We now come to a very well-defined group of species which may be called the "blue-winged ducks." They include the birds known as the blue-winged teals (*discors*, *cyanoptera*, *querquedula*) and the shovellers (*platalea*, *smithi*, *rhynchotis*, *clypeata*). The plumage pattern is consistent throughout the group, particularly the blue-gray color of the lesser and median wing coverts. Indeed, as we have said above, some of the species are very similar in plumage and differ mainly in body dimensions and bill size (*discors* and *rhynchotis; cyanoptera* and *platalea*). There are only minor differences in habits and display among the forms. They have a peculiar ceremony in which one or several pairs swim around in a circle, head to tail, merry-go-round-like, with the bill immersed and water running through it as if in a cooperative effort to stir up food. The same performance, in a formalized manner, occurs also as a courtship display. Another type of display is very simple, consisting in a rhythmical raising and lowering of the head by both male and female with the bill kept horizontal. Pursuit flight of several males after one female is of frequent occurrence. In the teals, *querquedula*, *discors*, and *cyanoptera*, the bill is long, but of normal shape; the voice of the drake is a harsh or whizzing clatter. The shovellers are larger and have the well-known huge spatulate bill.

Three species (*clypeata*, *rhynchotis*, and *smithi*) are similar in size, and the voice of the male is a low, short hoot: *took-took*. The South American Shoveller (*platalea*) is smaller and has a smaller bill; the male has a low, whizzing voice. We have found that when the Blue-winged Teal (*discors*) and the Cinnamon Teal (*cyanoptera*) are associated artificially they interbreed freely, producing fertile hybrids; and the stock soon becomes hopelessly mixed. The Common Shoveller (*clypeata*) and the Australian-New Zealand Shoveller (*rhynchotis*), as well as the three allied teals, have an eclipse plumage. The South American Shoveller (*platalea*) and Cape Shoveller (*smithi*) have no noticeable one. The Garganey drake (*querquedula*) is unique in the tribe in not acquiring its nuptial dress until late winter. All Cin-

namon drakes have an eclipse plumage, whether they come from North or South America. We made a point of importing birds from both continents to make certain of this fact, which had been questioned. It may be that the blue-winged ducks are linked to other river ducks through *Anas versicolor* (Group 3), whose wing pattern is very like that of the blue-winged group.

Group 14. Ringed Teal

A very puzzling species is the small Ringed Teal (*Anas leucophrys*), of South America. In its shape and general proportions, it is a normal *Anas*. Its plumage pattern and coloration, different in the two sexes, but very elaborate in both, is peculiar. Although the plumage of the male is very bright, it is not changed into an eclipse plumage after the breeding season. This is a perching, hole-nesting duck. In its display and courtship habits, it differs entirely from all other river ducks and resembles the pochards (Aythyini). As in those diving ducks, the female's call is a low, harsh, short, repeated *kur-r-r*. The male has a deep, soft whistle, which he emits while jerking back the neck, which is distended with air. He also indulges in the curious mock pursuit of the female, so typical of the pochards. Because of these strikingly different habits, Delacour (1936:369) placed the species in a special subgenus *Calonetta*. A better understanding of this little-known species may result in its generic separation.

Aberrant River Ducks

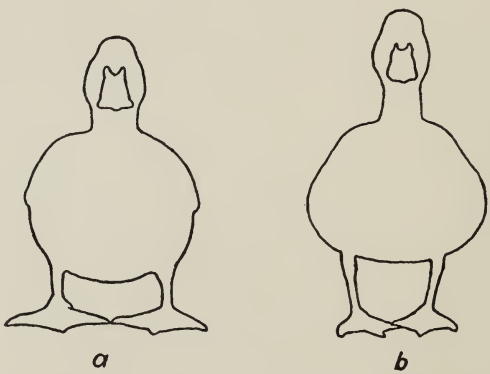
The curious Blue Duck (*Hymenolaimus malacorhynchos*) from New Zealand, with its peculiar coloration and bill, may be merely an aberrant *Anas*. It certainly belongs to the river duck group and shows no resemblance whatsoever to the Torrent Ducks (*Merganetta*). It is difficult to understand how such a suggestion could have ever been made. Its behavior is not well known, but it is reported to be able to dive. The downy young have a dark line through the eye as in the genus *Anas*.

The small Australian Pink-eared Duck (*Malacorhynchus membranaceus*) recalls in its plumage pattern and coloration the tropical pintails (Group 3), particularly the Marbled Teal (*angustirostris*). It has a white, not metallic, speculum. The large, peculiar bill differs widely from that of the shovellers and gives no clue to the systematist. The habits are little known and require further study before this duck can be assigned its proper place in the sequence of species.

Another puzzling species is the rare Pink-headed Duck from India (*Rhodonessa caryophyllacea*). It differs widely in coloration from all other ducks, with its blackish body, reddish-fawn speculum, pink head, pink hind neck, and bill. For many years we were able to observe live specimens in the collections at Clères and at Foxwarren, after Mr. A. Ezra had obtained a number of them from Calcutta.

These captive birds never nested, but they constantly displayed during the breeding season. The display of the drakes was simple: they puffed out the head feathers, with the neck shortened and resting on the back, then stretched the neck upward as they uttered a whizzing noise resembling the whistle of a mallard, though lower and weaker. The females showed in a rudimentary way the usual posture of river ducks. Because of the resemblance in display and posture, we consider this species as belonging to the present tribe. It has certainly no connection with the perching ducks, though one has often been suggested.

The Freckled Duck (*Stictonetta naevosa*), from Australia, is an aberrant, primitive species that defies any attempt at classification. In its general body build it seems to be closest to the river ducks, but the freckled color pattern and absence of speculum are peculiar, and the tarsus is reticulate in front. The trachea is quite different from that of the other river ducks. The bulla is absent, but the trachea has two expansions in the male. The color of the downy young and the various phases of the display have not yet been described. The food is obtained on the surface of the water, not by diving.



Leg position of (*a*) scaup and (*b*) mallard (*after Heinroth*).

3. TRIBE AYTHYINI. POCHARDS

This small tribe is composed of 14 species of fresh-water diving ducks. They are closely related to one another but can be divided into two genera. The color of the downy young and other characters indicate that the pochards are much more closely related to the river ducks than to the sea ducks.

They are characterized by a short, heavy body, a rather big head, and large feet. The legs are placed far back and laterally; the hallux is lobed. Sexual dimorphism is always present, but is sometimes not very pronounced. The males of all the temperate-zone species have an eclipse plumage which is usually intermediate between the nuptial

and the female plumage. Metallic colors do not occur on the wing, the speculum being either white or pale. The syrinx of the male has an asymmetrical bulla, but it is quite different from that of the river ducks; it is pointed rather than roundish, is more or less chambered inside, and has membranaceous windows on the outside. The downy young resemble those of many river ducks in color and pattern, but the yellow pigment is usually pronounced, and there is no distinct dark line through the eye. The heads are larger, even in the downy young, the legs and feet sturdier and set farther back on the body. Pochards come on land rather infrequently except for nesting; they walk clumsily. They are good divers although they usually do not stay under water so long as the sea ducks do. The food is primarily vegetable, but in certain species (Tufted Duck and scaups), and at certain seasons, the animal component prevails. All members of this tribe breed in their first year. The nest is placed on the ground among reeds or in the grass.

The display of pochards differs greatly from that of the river ducks and other tribes. The drakes have the curious habit of pursuing their own mates in a rough way. We have already referred to this mock brutality in connection with *Anas leucophrys*. The drakes in most species call very rarely. Females utter a loud *karr*. There is little basic difference among the displays of the various species of the tribe.

Hochbaum (1944:22–45), who describes the display in considerable detail for the Canvas-back (*"Nyroca" valisineria*), distinguishes four main postures of the displaying drake: (1) The "head-throw," during which the head is first thrown sharply backward until the top of the head touches the back and the throat points to the sky. Then after a brief, almost imperceptible pause, the head is snapped abruptly forward to swimming position. The call *ick, ick, cooo* is usually uttered during this motion. (2) The "neck-stretch," during which the drake raises his head as high as the stretched neck will permit and parades stiffly before the hen and the other drakes. (3) The "sneak," in which the drake stretches head and neck horizontally on the water. (4) The "threat," in which the drake swims in a crouched position, usually when ready for a fight. The "head-throw," during which the neck seems to be inflated with air, apparently occurs in one form or another in all the species of this genus.

The genus *Netta* is composed of three species inhabiting temperate and subtropical regions. They constitute a bridge between the river ducks and the more specialized pochards of the genus *Aythya*[5] being less well adapted to diving than the latter. The body is longer and narrower, the legs longer and more slender, the bill narrower, than in *Aythya*, and the birds are less heavy and clumsy on land. All three

[5] *Aythya* has priority over *Nyroca* and is not preoccupied by *Aethia* (see Witherby *et al.*, 1939:286).

species have bright red eyes. They are the Red-crested Pochard (*Netta rufina*) of southern Europe and central Asia; the Rosy-billed Pochard of Argentina ("*Metopiana*" *peposaca*); and the Southern Pochard ("*Nyroca*" *erythrophthalma*)[6]. The species *rufina* and *peposaca* are usually placed in separate monotypic genera, while *erythrophthalma* is united with *Aythya* on account of a similarity in color to several species of that genus. But in its proportions and its plumage pattern *erythrophthalma* is obviously close to *peposaca*. The display of these two species is on the whole that of the other pochards, except that *peposaca* sometimes calls with neck vertical and bill pointing skyward. The male Red-crested Pochard (*rufina*) has rather different postures, particularly one in which it spreads its long head feathers, depresses the bill, and rests the neck on the back while uttering a sneezing call. This resembles a simple phase of the display of the mallard. The trachea of *rufina* has two bulbous enlargements.

The genus *Aythya* contains four groups: The first consists of the closely related Canvas-back (*valisineria*), the European Pochard (*ferina*), and the Redhead (*americana*). The European Pochard in coloration is intermediate between the other two, but in the shape of its head it is nearer to *valisineria* than to *americana*. Group 2, the white-eyes, contains the four species, *innotata* (Madagascar), *nyroca* (Eurasia), *baeri* (east Asia), *australis* (Australia and New Zealand), all from temperate and subtropical lands. Although superficially similar, their postures and proportions are different enough to justify considering them separate species. The black and white Tufted Duck (*fuligula*), from Eurasia, and the Ring-neck (*collaris*), from North America, are certainly related to each other, and they form a third group which includes also the New Zealand Duck (*novae-seelandiae*). Group 4 consists of the scaups. The Greater Scaup (*marila*), which ranges all over the northern hemisphere, is the most heavily built bird and ablest diver of the tribe and the only one that spends much time on the ocean. The Lesser Scaup (*affinis*), restricted to America, is closely related. The scaups apparently take a higher proportion of animal food than the other species of the pochard tribe.

4. TRIBE CAIRININI. PERCHING DUCKS

This very peculiar group of ducks had already been separated by Salvadori, as a subfamily (Plectropterinae), and, in our opinion, it was a mistake of modern authors to remove from it the Mandarin ("*Dendronessa*" *galericulata*) and the Carolina Wood Duck (*Aix sponsa*) and place them among the river ducks. In their general proportions and

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[6] The Southern Pochard has a curious distribution in East and South Africa and in South America, where it is currently stated to inhabit only the northwestern parts. But it evidently occupies a much greater area, for a number of live specimens were received at Clères in 1938 from the neighborhood of Pernambuco, eastern Brazil.

shape, in habits and behavior, they clearly belong to the perching ducks. To the 14 species listed by Salvadori, several of which we relegate to the rank of subspecies, we have added three more. One of these is the very aberrant Pied Goose (*Anseranas*); peculiar as it is, it resembles the Spur-winged Goose (*Plectropterus*) in general aspect and habits; it appears to be certainly nearer to that than to any other species of Anatidae. We also consider the Brazilian Teal (*Amazonetta*) a member of this tribe on account of the general proportions of its wings and tail, the position of its legs (alike in adults and young), its voice, display, and its living and nesting habits. Finally, we place here, provisionally at least, the small aberrant Australian Maned Goose (*Chenonetta jubata*). It has usually been considered allied to *Chloëphaga* (Tadornini), but its behavior and habits, as well as the pattern of the downy young, which is very similar to that in the Mandarin Duck and totally different from those in the sheldrake tribe, indicate that it would be a mistake to leave it with the sheldrakes.

The nearest relatives of the perching ducks seem to be the river ducks. The two groups resemble each other greatly in the coloration of the downy young and in the structure of the syrinx. Hybrids between species of the two tribes are sterile, but females of the Mallard × Muscovy cross sometimes lay small eggs. Serological tests confirm this relationship (Sokolovskaia, 1936). Species such as *Amazonetta brasiliensis*,[7] *Aix sponsa*, and *Aix galericulata* seem to bridge the gap between the river ducks and the perching ducks.

The perching ducks spend more time in trees than any others, and most of them nest in holes high above the ground. They are decidedly forest ducks. Correlated with these habits are their unlobed well-developed hallux and their sharp, strong claws. The legs are set more forward than in the river ducks, in fact even more than in the geese and the sheldrakes. The length of the tarsus varies from very long (e.g. *Plectropterus*) to extremely short (e.g. *Nettapus*). The bill is rather thick and never depressed, often very strong, with a large nail. The rectrices are wide and long, and the tail is only slightly graduated, never pointed. The wings are very broad and brightly colored. The scapulars, secondaries, and particularly the tertiaries, are notably developed. In a number of species metallic colors occur extensively in the plumage, although there is no sharply defined speculum; the tertiaries and wing coverts are metallic or of a bright color. A bony, spur-like knob at the bend of the wing is more or less well developed in most species. The young are remarkable for their long, stiff tails and their ability to climb. They have no very particular pattern of down; all are brown and

[7] *Amazonetta vittata* Derscheid, 1938, is apparently a synonym (see Zimmer and Mayr, 1943, *Auk*, 60:250).

yellow, except those of the pygmy geese (*Nettapus*), and have an eye-line. With the exception of the two species of *Aix*, perching ducks inhabit the tropics and subtropics. Their display is usually very simple, almost nonexistent, consisting mainly in a forward and backward movement of the head with neck extended.

In general, the voice of the drake is a low, squeaking or aspirated, whistle, and the female quacks harshly. Many species are remarkably silent. Only three species have an eclipse plumage. In most perching ducks, the female is rather similar to the male, but in some cases it is strikingly smaller. Many of the species, if they pair at all, seem to have very weak mating ties.

It is only with great reservations, as we have said before, that we list among these birds the queer and primitive Australian Pied Goose (*Anseranas semipalmata*) in which the two sexes have a loud voice and are alike except for a slight difference in size. There is no sign of a real display in this species. They perch high up, an action facilitated by their semipalmate feet and long hallux, and they spend much time on trees. They appear, however, to nest on the ground, among rushes. They have long legs, a powerful bill, and a bald forehead, resembling *Plectropterus* in most of their features (Figures 11 and 12). *Anseranas* differs from all other Anatinae, except *Cereopsis* and *Stictonetta*, in its reticulated tarsi, thus approaching the Anserinae. It is unique among the Anatidae in having a gradual wing molt. The downy young resembles that of *Plectropterus*.

The African Spur-winged Goose (*Plectropterus gambensis*) is also long-legged, has a bare forehead, adorned with a knob, and big spurs on the bend of the wing. We have seen scores of them perching on small limbs high up in large trees in West Africa. They are reported to lay usually on the ground, but also in old nests in trees. The male has a curious high-pitched voice, which it uses incessantly, though the female seems almost mute. They have a small bulla on the syrinx. They are extremely aggressive and sometimes injure other waterfowl considerably with their sharp spurs.

The Comb Duck (*Sarkidiornis melanotos*) includes two well-marked subspecies, one (*melanotos*) extending from Africa to southeast Asia (Figure 13), the other (*carunculatus*) inhabiting South America. We have observed at Clères that the racial hybrids are not intermediate. In such hybrid broods some birds look like pure *melanotos* and others like pure *carunculatus*. Comb Ducks have legs of moderate length; they perch freely and nest in tree holes. No pair formation seems to exist, the males pursuing and mating with any available female as the Muscovies do. The difference in size between the drake and the duck is truly astonishing. Both sexes are almost mute, the male having a weak whistle and the female a low grunt. The display of the male, which is also his challenge, consists in lifting

the neck and chest, with wings slightly raised, the head slowly moved from side to side, the neck curved and dipped downward at frequent intervals. According to Heinroth, the male initiates his pursuit of females often with "dipping" displays such as occur in the geese. The female has no display whatever, according to our observations at Clères. Contrary to current descriptions, the downy young are brown and yellow, much like those of *Cairina* and *Plectropterus*, and have no white or other distinctive head markings. Erroneous descriptions found in the literature seem to have been based on wrongly identified specimens in the British Museum.

We consider that the three large, tropical, short-legged forest species which biologically replace one another in America (*Cairina moschata*), Africa (*"Pteronetta" hartlaubi*), and southeast Asia (*"Asarcornis" scutulata*) are congeneric. All have the same proportions of the body, wings, tail, bill, and feet. The males of all three have, in the breeding season, a swollen knob at the base of the bill; they agree fairly well in general pattern and perfectly in that their wings all have a showy patch formed by the upper wing coverts. The males are considerably larger than the females, although the difference is not so striking as in the Comb Duck. The two sexes are similar in coloration. The habits of the three species are very much alike; they spend a great part of the day perched on large trees, in the holes of which they nest. They appear to be promiscuous, although more remains to be learned of their behavior in a wild state. They are very quarrelsome. When the characters invoked for the generic distinction of these three species are examined, they appear quite insufficient, and we therefore consider *Asarcornis* and *Pteronetta* as synonyms of *Cairina*.

The Muscovy Duck (*Cairina moschata*), common in Central and South America, is the best known of the three. The voice of the drake is a low blowing hiss; the female has a harsh quack, seldom heard. The male display consists of a rhythmic bobbing forward and backward of the head, with the crest spread, the neck extended, the wings slightly lifted, and the long tail vibrating. The female answers in a similar but less marked way.

The White-winged Duck (*C. scutulata*) has very similar display and habits. The voice is said to be loud in both sexes, but we never heard ours emit any sound other than weak grunts. Both this species and the Muscovy have conspicuous white wing coverts.

The West African Hartlaub's Duck (*C. hartlaubi*) is smaller, but seems to have the same general habits. The loud quacking reported of the species is probably that of the female. We have not made an adequate study of this species in life. In proportions and color pattern, it is very close to the Muscovy and White-winged Ducks. Its upper wing coverts are blue-gray instead of white.

The anomalous Brazilian Teal (*Amazonetta* ["*Anas*"] *brasiliensis*) probably earns its logical place with the Cairinini, for it seems to be a dwarf *Cairina*, resembling that genus in general shape and proportions, and even in habits. Like them, it is a tropical forest bird. The display of the male is so simple as to consist merely in a lifting of the neck, as he whistles loudly. The female quacks briefly and moves her head up and down, slightly sidewise. Male and female differ in plumage and in the color of the bill, but both are rather bright, and there is no eclipse plumage. The downy young looks like a miniature young Muscovy.

The three genera *Chenonetta*, *Aix*, and *Nettapus* have a smaller, smoother, and less flat bill, recalling those of *Branta* and of *Chloëphaga*, but this is of no special taxonomic importance. *Chenonetta* has long legs and looks like a small goose; *Aix* has rather short legs like those in *Cairina*, while *Nettapus* has legs so short that the birds are almost unable to walk.

Because of the great similarity of the females, it seems entirely unnecessary to separate generically the Mandarin and the Carolina Wood Duck, and we combine them in the genus *Aix*. As we have explained above, both these birds have the body proportions, voice, and habits of the tribe, and they are far from all the river ducks. A curious fact to be recorded is the inability of these two allied species to produce hybrids, although when associated in captivity they pair freely. There is a slight but not important difference in the voice and display of the two birds. The Mandarin drake has the more complicated posture: he lifts his wing fans and crest and blows up his chest, slowly lowers his head until his bill touches the water, then jerks his head back quickly with a short, subdued, snorting whistle, *uib*. Several drakes perform together with many short flights and perchings. The female answers with movements of her neck and head. In the Wood Duck, the male just raises his crest, arches his neck, and bows, with softer and more frequently repeated whistles, *jiib, jiib*. He never displays in company with other males. The female behaves much like the Mandarin, but she calls more often and has a softer, more melodious voice. Both Mandarin and Wood Duck form strongly attached pairs (Heinroth, 1910). The downy young of *Aix galericulata* resembles that of *Cairina*, but is paler and duller and has an additional dark stripe below the eye, as in *Chenonetta*.

It is very difficult to assign a place to the small Australian species, *Chenonetta jubata*, usually known as the Maned Goose, but also called locally the Wood Duck. It has a certain superficial resemblance to the species of *Chloëphaga*, but is smaller and differs widely from them in its habits, behavior, and display. Furthermore, the downy young is brown and yellowish and has almost the same shape and color pattern as the young Mandarin Duck, including the dark parallel

face lines. This seems to indicate its real affinity. The pattern is totally different from the bold grayish- or blackish-brown and white pattern which is so characteristic of the young in *Chloëphaga* and allied genera.

Like the other members of the present tribe, the Maned Goose is a tree-perching, hole-nesting bird. The voice of the male is a low, whizzing whistle, that of the female a soft quack, drawn out with a special modulation like a mew. The display of the male is simple, consisting in raising the head and neck, as he calls and puffs out his mane; that of the female is *Anas*-like, a sidewise movement of the head with neck extended, as in the Mandarin and Carolina Wood Ducks. The females sometimes engage in "incitement displays," like certain river ducks and sheldrakes. *Chenonetta* has a short, smooth bill, much like that of *Chloëphaga* and *Branta*, but also similar to that of the genus *Nettapus*, and not very different from those of the Mandarin and Carolina Wood Ducks. Its legs are rather long, like those of *Sarkidiornis*, but much more slender, and it walks easily and daintily. It is very gentle in temperament.

The pygmy geese (*Nettapus*) are the smallest members of the family, and also some of the most beautiful. They have small *Branta*-like bills and such extremely short legs that they can hardly progress on land. They perch freely, fly and swim well. All three species are tropical. They have much white and green in the plumage, and the sexes are slightly but clearly different. One species (*N. coromandelianus*) has a well-marked breeding plumage in the male. The downy young of the pygmy geese are of the usual shape for the tribe, but have peculiar dark gray and white patterns. As in the genus *Aix*, the downy young vary from species to species.

The African Pygmy Goose (*Nettapus auritus*) has a thick bill. In both sexes the display is much like that of the Wood Duck, as we have often observed in the wild in Madagascar and in captivity at Clères. Its voice is a soft whistle in the male, a weak quack in the female.

The Green Pygmy Goose (*N. pulchellus*), of Australia, is little known, but seems to be similar in voice and display to the African species.

The Indian Pygmy Goose, or "Cotton Teal" (*N. coromandelianus*), whose range extends from India to Australia, has a flatter bill, is still smaller, and has several peculiarities, notably a breeding plumage which the male assumes for only a few months. The male's voice is a curious rattling cackle, and both sexes have a quick "nervous" jerking of the neck. The display of the male is elaborate, consisting of an arching of the neck, with a partial opening of the wings, showing the white patches on the primaries.

5. TRIBE MERGINI. SEA DUCKS

The various tribes of diving ducks are completely different in proportions, pattern, and habits. The sea ducks show no close relationship with the pochards or the stiff-tailed ducks. Their lobed hallux, a functional adaptation, is of little phylogenetic significance.

Delacour (1936:376), as well as Heinroth and other authors, has pointed out the obvious relationship of the mergansers (*Mergus*) with the golden-eyes (*Bucephala*); and in spite of the wide difference between the extreme forms of the tribe (*Mergus* and *Somateria*), the sea ducks form one of the most closely knit subdivisions of the anatine subfamily. The seven genera are connected with one another by intermediate species. The Hooded Merganser (*Mergus cucullatus*), for example, connects the larger mergansers, through the Smew (*"Mergellus" albellus*) and the Buffle-head (*Bucephala albeola*) to the golden-eyes. The Harlequin (*Histrionicus*) is a link between the Old-squaw (*Clangula*) and the scoters (*Melanitta*), as is the Labrador Duck (*Camptorhynchus*) between the Old-squaw and the eiders (*Somateria*).

On the other hand, the golden-eyes, the Old-squaw, and the Harlequin are undoubtedly related, as is proved by the same bold pattern of dark gray and white of all their downy young. The downy young of the White-winged Scoter (*Melanitta fusca*) is also very similar and thus connects the whole group to the other species of the genus (*M. perspicillata* and *"Oidemia" nigra*). In turn, the downy young of the last two species link them to the eiders, all being brown above, white underneath, without strong markings. Also, immature Surf (*perspicillata*) and White-winged Scoters closely resemble immature Harlequins in their general color as well as in their white head markings, which are already suggested by the white patch on the sides of the head in the Buffle-head.

The ducks of the tribe Mergini are rather isolated, but, in our opinion, they are closer to the Cairinini than to any others. The nesting habits of the mergansers and the golden-eyes, their long and broad tails and their general behavior are suggestive of a certain affinity between the two tribes, which is corroborated by the attraction that such birds as the Mandarin and Wood Ducks exert on golden-eyes and Harlequins when they are associated on a lake.

The birds of this tribe, with a very few exceptions, spend a part of their time at sea, and animal life constitutes their principal food. They all are great divers. Their bill is strong, with a large hooked nail, and varies from long, thin, and narrow to thick and short, according to their principal food (fish, mussels, etc.). Their wings are short and their flight heavy, and they walk with some difficulty, the eiders being less clumsy on land than the others.

The majority of the species nest in the hollows of trees, in holes and crevices in rocks, or any other sort of deep shelter. Some of the

scoters and eiders, however, deposit their eggs on the ground in the open, among grass and bushes.

All male Mergini are brightly colored and have a distinct eclipse plumage, the scoters, which are prevailingly black, and the two dull-colored southern mergansers being exceptions. They are not adult before their second or third year. In some cases, the females show a definite change in colors according to the season. There is no metallic color in the beautiful plumage of the drakes, not even in the speculum. Iridescent gloss occurs only on the head of the golden-eyes and mergansers and on the speculum of Steller's Eiders.

Sea ducks are very silent birds as a rule, even the females; female eiders, however, utter frequently a harsh grunting cackle. Some of the others utter a similar cackle during the breeding season; at that time, the males emit low, subdued, ventriloquial grunts or whistles, differing from species to species. The only noisy drake is the Old-squaw, which calls loudly in all seasons. The sea ducks generally have very elaborate displays which have little resemblance to those of any other Anatinae, except perhaps to some of the postures of the stiff-tailed ducks. All sea ducks live in the cold or temperate parts of the northern hemisphere, with the curious exception of two rare southern mergansers inhabiting Brazil (*octosetaceus*) and the Auckland Islands, south of New Zealand (*australis*).

The four species of eiders (*"Polysticta" stelleri*, *"Arctonetta" fischeri*, *Somateria spectabilis*, and *S. mollissima*), although closely related to one another, stand somewhat apart from the other sea ducks. The syrinx has a structure like that in the river ducks, and the downy young lack the black cap typical of most sea ducks. We reject the peculiarity of the bill of Steller's Eider (*S. stelleri*) as a valid generic criterion. The four species agree closely in color pattern, and in the nature of their feathers, notably in the velvety-green and grayish-blue ones of the head and the long, curved ornamental secondaries. The peculiar green pigment on the head of the male is a unique feature of this genus. The females of the four species are much alike. All eiders are ground nesters and breed usually near the sea-shore, but also on the arctic tundra, near fresh-water pools. The Old-squaws, Harlequins, scoters, and eiders resemble the mergansers and golden-eyes in voice as well as in display, though the display is simpler, consisting of stretching the neck and calling, with an upward jerk of the bill.

The extinct Labrador Duck (*Camptorhynchus*) seems to be about halfway between the eiders and the Old-squaw. The male is colored more like an eider, the female more like a scoter or Old-squaw.

The three scoters (*Melanitta*, including *"Oidemia"*) form a very compact group, and it would be misleading to divide the group into several genera merely because each of the three species has certain structural peculiarities (Miller, 1926). The Common Scoter (*M.*

nigra) has an even more strongly emarginate first primary than the male golden-eye. It has about the simplest syrinx, with no bulla and no enlargement of the trachea. The White-winged Scoter (*M. fusca*) and Surf Scoter (*M. perspicillata*) have a big, bulb-like inflation of the trachea.

The genera *Clangula* (Old-squaw) and *Histrionicus* (Harlequin) occupy a central position among the sea ducks. They lead to the scoters and eiders on one side and to the golden-eyes and mergansers on the other. *Clangula* is by far the more vocal of the two, but otherwise the displays of the two genera are very similar. It has been claimed repeatedly that the Old-squaw has two "eclipse" plumages, the first one acquired by partial molt, February–May; the second, also by partial molt, late July–August. However, as Sutton (1932, *Auk*, 49:42–51) has shown, two eclipse plumages are merely simulated by the protracted postnuptial molt. Both species are ground nesters, although the Harlequin is reported to nest occasionally in holes in trees or in cliffs.

The golden-eyes (*Bucephala*) nest in holes in trees and are more partial to fresh water than the previously discussed genera of this tribe. The courtship displays of the males are very elaborate, but on the whole very much like those of the mergansers (see below). In fact, except for the shape of the bill, the golden-eyes are exceedingly close to *Mergus*. Female Common Golden-eyes (*clangula*) and Barrow's Golden-eyes (*islandica*) resemble female mergansers closely in general color pattern; and their downy young are like those of the mergansers except that the black cap extends below the eye and the cheeks are pure white. Hybrids between *Bucephala clangula* on one side, and *Mergus albellus* (Smew) and *M. cucullatus* (Hooded Merganser) on the other side, have been found repeatedly in the wild state, indicating the close affinity of the golden-eyes and mergansers. The syrinx in the two genera, with large bullae, and the inflated bulbs of the trachea, are additional proof of this relationship. The Smew lacks the enlargement of the trachea and has a smaller bulla. We have found no description of the syrinx of the Hooded Merganser or the Buffle-head.

The mergansers (*Mergus*) are well characterized by their long, thin saw-bill. Nothing is known of the nesting of the three rarer species (*squamatus*, *australis*, *octosetaceus*). The Red-breasted Merganser (*serrator*) nests on the ground among rocks and in depressions. The other three species (*albellus*, *cucullatus*, and *merganser*) nest by preference in tree holes. The display varies with each species, but consists generally of the following main features: (1) sudden rapid stretching of head and neck upwards, bill gaping, and quick return to normal position; (2) rising on water, beak touching breast; (3) spasmodic movement of feet, throwing up a spurt of water behind. The whole display is associated with a raising of the crest, bowing,

splashing, and chasing. Females have a simpler display, reproducing some of the male's postures in a rudimentary way.

The downy young are dark brown above, white below, with a bold pattern resembling that of the golden-eyes, but they have a rusty tinge on the sides of the head, except in the Smew.

Unlike all other ducks, mergansers are adapted to the chase of moving prey. Their body is more streamlined than that of their nearest relatives, the golden-eyes. This difference in form is particularly apparent in the sternum. In this connection also, the Smew and the Hooded Merganser seem to be somewhat intermediate between the more typical mergansers and the golden-eyes. We cannot see any good reason for a generic division of the merganser group.

6. TRIBE OXYURINI. STIFF-TAILED DUCKS

This curious tribe of diving ducks has no apparent close connection with any other. Their rectrices are long and stiff, and their tail coverts are very short. The nail of their broad and depressed bill is hooked and sharp. Their legs are placed so far back on the body that they can walk only with difficulty. The neck is short and very thick. In the northern species, the postnuptial molt produces a dull plumage that is replaced in the spring by a bright prenuptial plumage. The downy young have a peculiar pattern. Stiff-tailed ducks are almost voiceless in ordinary times, but the drakes, during their courtship, emit a variety of squeaking and clucking noises. Their display is striking: they lift their tails, and puff out their chests; then, stretching their necks forward and backward, they slap their bills on their inflated chests. They also press their bills on their lifted and puffed chests, with the tail down in the water, and finally with both feet they kick water, which spurts backwards. The females stretch out their necks with their bills open.

They lay the largest of all known duck eggs. They build large and elaborate nests among reeds and rushes. The male assists his mate in the care of the young. With their small wings, these ducks have a labored flight, but they are marvelous divers. They feed mostly on vegetable material, although they like animal food as well.

The North American Ruddy Duck (*Oxyura jamaicensis*) is migratory, as is the larger and duller White-headed Duck (*O. leucocephala*) which lives around the Mediterranean Sea and in Central Asia. The small Masked Duck (*dominica*) from the West Indies and tropical America is undoubtedly congeneric; no valid character has ever been pointed out to support the genus *Nomonyx* that was proposed for this species. The tropical forms from South America (*ferruginea, vittata*), Africa (*maccoa*), and Australia (*australis*) are so similar in every respect that they must be listed as subspecies of *O. australis*. We believe that the ranges of *ferruginea* and *vittata* do not overlap during the breeding season.

The weird Australian Musk Duck (*Biziura lobata*) is certainly a member of this group, in spite of its thick bill and carnivorous habits. Its display is like that of typical members of the group.

The African White-backed Duck (*Thalassornis*), also found in Madagascar, appears very different, but its plumage pattern recalls that of the female Masked Duck. In color pattern, the downy young are somewhat different from those of *Oxyura* but resemble them in shape and structure of the tail. Delacour has observed the species at length, in the wild and in captivity. They are strange little birds, always found in pairs or families, quarrelsome, very sedentary and inactive. We seldom saw one fly, but they dive with great ease. They cannot walk, and they swim slowly. They have no noticeable display, and the two sexes are alike in coloration. Their necks are comparatively long, and they often stretch them to full length. Their voice is a harsh whistle which recalls that of certain *Dendrocygna*. They further differ from *Oxyura* in their very short tails.

Even more aberrant is the parasitic Black-headed Duck (*Heteronetta atricapilla*) from South America. It differs from typical stiff-tailed ducks in that it lacks a lobe on the hind toe, and has a fairly soft, short tail and elongated upper tail coverts, smaller feet and a narrower bill. On the other hand, as Wetmore (1926:84) has pointed out, *Heteronetta* agrees with the Oxyurini "in the full, loose skin of the neck, development of special, distensible sacs about the head in the male, small wings, glossy, shining plumage, and lack of a bulla ossea." The color pattern is very much like that of females of *Oxyura*. They dive as well as members of the genus *Oxyura* do, and swim like them except that the tail is not held at an angle. The eggs are huge, relative to the size of the female, and the parasitic habits of this species are foreshadowed by the semiparasitic habits of other members of the Oxyurini (Friedmann, 1932). The downy young of *Heteronetta* has apparently not yet been described.

7. TRIBE MERGANETTINI. TORRENT DUCKS

The Andes are the home of a very curious species of small duck with a narrow bill, a long, stiff tail, and sharp spurs at the bend of the wing. They live along rapid mountain streams, dive with considerable skill, perch on rocks, and nest in crevices. In the present state of our knowledge, it is difficult to assign them a place, but they are certainly not closely related to the mergansers, and may rather be aberrant relatives of the stiff-tailed ducks. The plumage of the adults (different in the two sexes but elaborate in both), and the pattern of the downy young, are striking and peculiar. The structure of the syrinx and the courtship habits are apparently unknown.

The genus has been thoroughly revised by Conover (1943, *Field Mus. Nat. Hist. Zool. Ser.*, 24:345–356). It seems to us, however, that the geographical forms of *Merganetta armata* are not sufficiently distinct to justify the recognition of three separate species. We follow Hellmayr, Hartert, and Peters in considering them conspecific.

A List of the Genera and Species of Anatidae

On the basis of the considerations in the above section of our paper, we propose the following list[8] of genera and species of Anatidae:

I Subfamily Anserinae

1. tribe anserini. geese and swans

Branta
- *canadensis*, Canada Goose
- *sandwicensis* ("*Nesochen*"), Hawaiian Goose
- *leucopsis*, Barnacle Goose
- *bernicla*, Brant
- *ruficollis*, Red-breasted Goose

Anser
- *cygnoides* ("*Cygnopsis*"), Swan-goose
- *fabalis* (inc. *neglectus* and *brachyrhynchus*), Bean Goose, Sushkin's Goose, and Pink-footed Goose
- *albifrons*, White-fronted Goose
- *erythropus*, Lesser White-fronted Goose
- *anser*, Grey-Lag Goose
- *indicus* ("*Eulabeia*"), Bar-headed Goose
- *canagicus* ("*Philacte*"), Emperor Goose
- *caerulescens* ("*Chen*", inc. *hyperboreus* and *atlanticus*), Blue Goose, Lesser and Greater Snow Geese
- *rossi* ("*Chen*"), Ross's Goose

Cygnus
- *columbianus* (inc. *bewicki*), Whistling and Bewick's Swans
- *cygnus* (inc. *buccinator*), Whooper and Trumpeter Swans
- *melanocoryphus*, Black-necked Swan
- *olor*, Mute Swan
- *atratus* ("*Chenopis*"), Black Swan

Coscoroba
- *coscoroba*, Coscoroba

2. tribe dendrocygnini. whistling ducks (tree ducks)

Dendrocygna
- *arborea*, Black-billed Whistling Duck
- *guttata*, Spotted Whistling Duck
- *autumnalis*, Red-billed Whistling Duck
- *javanica*, Indian Whistling Duck
- *bicolor*, Fulvous Whistling Duck
- *arcuata*, Wandering Whistling Duck
- *eytoni*, Plumed Whistling Duck
- *viduata*, White-faced Whistling Duck

[8] Additional genera and species recognized by Peters are given in parenthesis. Each pair or group of species united by a bracket constitutes a superspecies.

II Subfamily Anatinae

1. tribe tadornini. sheldrakes

Lophonetta
specularioides ("*Anas*"), Crested Duck

Tadorna
cristata ("*Pseudotadorna*"), Korean Sheldrake
ferruginea ("*Casarca*"), Ruddy Sheldrake
cana ("*Casarca*"), South African Sheldrake
tadornoides ("*Casarca*"), Australian Sheldrake
variegata ("*Casarca*"), Paradise Sheldrake
radjah, Radjah Sheldrake
tadorna, Common Sheldrake

Alopochen
aegyptiacus, Egyptian Goose

Neochen
jubatus, Orinoco Goose

Cyanochen
cyanopterus, Abyssinian Blue-winged Goose

Chloëphaga
melanoptera, Andean Goose
poliocephala, Ashy-headed Goose
rubidiceps, Ruddy-headed Goose
picta (=*dispar*=*leucoptera*), Magellan Goose
hybrida, Kelp Goose

Aberrant Species

Cereopsis
novae-hollandiae, Cape Barren Goose

Tachyeres
patachonicus, Flying Steamer Duck
pteneres, Magellanic Flightless Steamer Duck
brachypterus, Falkland Flightless Steamer Duck

2. tribe anatini. river ducks

Anas
specularis, Bronze-winged Duck

Anas
waigiuensis ("*Salvadorina*"), Salvadori's Duck

Anas
angustirostris, Marbled Teal
capensis, Cape Teal
punctata, Hottentot Teal
versicolor, Versicolor Teal
erythrorhyncha, African Red-billed Duck
bahamensis (inc. *galapagensis*), Bahama and Galápagos Island Ducks

Anas
- *georgica* (inc. *spinicauda*), South Georgian and South American Pintails
- *acuta* (inc. *eatoni*), Common Pintail and Eaton's Pintail

Anas
- *flavirostris* (inc. *andium*), Yellow-billed and Andean Teal
- *crecca*, Green-winged Teal

Anas
- *formosa*, Baikal Teal

Anas
- *falcata*, Falcated Teal

Anas
- *bernieri*, Madagascan Teal
- *gibberifrons* (inc. *albogularis*), Gray Teal and Andaman Teal
- *castanea*, Chestnut-breasted Teal
- *aucklandica* ("*Nesonetta*", inc. *Anas chlorotis*), Auckland Island Teal and Brown Teal

Anas
- *fulvigula* (inc. *diazi* and *rubripes*), Dusky Duck, Mexican, and Black Ducks
- *poecilorhyncha* (inc. *superciliosa* and *luzonica*), Spot-bill, Australian Duck, and Philippine Duck
- *melleri*, Meller's Duck
- *undulata*, African Yellow-billed Duck
- *platyrhynchos* (inc. *wyvilliana*, *laysanensis*, and *oustaleti*), Common Mallard, Hawaiian Duck, Laysan Teal, and Marianas Mallard

Anas
- *sparsa*, African Black Duck

Anas
- *strepera* ("*Chaulelasmus*", inc. *couesi*), Gadwall and Coues' Gadwall

Anas
- *penelope* ("*Mareca*"), European Widgeon
- *americana* ("*Mareca*"), American Widgeon
- *sibilatrix* ("*Mareca*"), Chilöe Widgeon

Anas
- *discors*, Blue-winged Teal
- *cyanoptera*, Cinnamon Teal
- *querquedula*, Garganey Teal
- *platalea* ("*Spatula*"), South American Shoveller
- *smithi* ("*Spatula capensis*"), Cape Shoveller
- *rhynchotis* ("*Spatula*"), Australian-New Zealand Shoveller
- *clypeata* ("*Spatula*"), Common Shoveller

Anas
leucophrys, Ringed Teal

Aberrant Species

Hymenolaimus
malacorhynchos, Blue Duck
Malacorhynchus
membranaceus, Pink-eared Duck
Rhodonessa
caryophyllacea, Pink-headed Duck
Stictonetta
naevosa, Freckled Duck
(Removed from *Anas: specularioides*, see *Lophonetta*, Tribe Tadornini; *brasiliensis*, see *Amazonetta*, Tribe Cairinini).

3. TRIBE AYTHYINI. POCHARDS

Netta
rufina, Red-crested Pochard
peposaca ("*Metopiana*"), Rosy-billed Pochard
erythrophthalma ("*Nyroca*"), Southern Pochard
Aythya
valisineria ("*Nyroca*"), Canvas-back
ferina ("*Nyroca*"), European Pochard
americana ("*Nyroca*"), Redhead
innotata ("*Nyroca*"), Madagascan White-eyed Duck
nyroca ("*Nyroca*"), Common White-eyed Duck
baeri ("*Nyroca*"), Baer's White-eyed Duck
australis ("*Nyroca*"), Australian White-eyed Duck
novae-seelandiae ("*Nyroca*"), New Zealand Duck
collaris ("*Nyroca*"), Ring-necked Duck
fuligula ("*Nyroca*"), Tufted Duck
affinis ("*Nyroca*"), Lesser Scaup
marila ("*Nyroca*"), Greater Scaup

4. TRIBE CAIRININI. PERCHING DUCKS

Amazonetta
brasiliensis ("*Anas*"), Brazilian Teal
Chenonetta
jubata, Maned Goose
Aix
galericulata ("*Dendronessa*"), Mandarin Duck
sponsa, Carolina Wood Duck
Nettapus
auritus, African Pygmy Goose
pulchellus ("*Cheniscus*"), Green Pygmy Goose
coromandelianus ("*Cheniscus*"), Indian Pygmy Goose
Sarkidiornis
melanotos (inc. *carunculatus*), Comb Duck

Cairina
hartlaubi ("*Pteronetta*"), Hartlaub's Duck
scutulata ("*Asarcornis*"), White-winged Duck
moschata, Muscovy Duck
Plectropterus
gambensis, African Spur-winged Goose

Aberrant Species

Anseranas
semipalmata, Pied Goose

5. TRIBE **MERGINI.** SEA DUCKS

Somateria
mollissima, Common Eider
spectabilis, King Eider
fischeri ("*Arctonetta*"), Spectacled Eider
stelleri ("*Polysticta*"), Steller's Eider
Camptorhynchus
labradorius, Labrador Duck
Melanitta
nigra ("*Oidemia*"), Common Scoter
perspicillata, Surf Scoter
fusca, White-winged Scoter
Histrionicus
histrionicus, Harlequin Duck
Clangula
hyemalis, Old-squaw
Bucephala
islandica, Barrow's Golden-eye
clangula, Common Golden-eye
albeola, Buffle-head
Mergus
albellus ("*Mergellus*"), Smew
cucullatus ("*Lophodytes*"), Hooded Merganser
octosetaceus, Brazilian Merganser
australis, Auckland Island Merganser
serrator, Red-breasted Merganser
squamatus, Scaly-sided Merganser
merganser, Goosander

6. TRIBE **OXYURINI.** STIFF-TAILED DUCKS

Oxyura
dominica ("*Nomonyx*"), Masked Duck
leucocephala, White-headed Duck
jamaicensis, North American Ruddy Duck
australis (inc. *maccoa*, *ferruginea*, and *vittata*), Blue-billed Duck, Maccoa Duck, Peruvian Ruddy Duck, and Argentine Ruddy Duck

Biziura
lobata, Australian Musk Duck

Aberrant Species

Thalassornis
leuconota, African White-backed Duck
Heteronetta
atricapilla, Black-headed Duck

7. TRIBE MERGANETTINI. TORRENT DUCKS

Merganetta
armata, Torrent Duck

GENERA RECOGNIZED BY PETERS AND SYNONYMIZED HERE

Arctonetta = *Somateria*
Asarcornis = *Cairina*
Casarca = *Tadorna*
Chaulelasmus = *Anas*
Chen = *Anser*
Cheniscus = *Nettapus*
Chenopis = *Cygnus*
Cygnopsis = *Anser*
Dendronessa = *Aix*
Eulabeia = *Anser*
Lophodytes = *Mergus*
Mareca = *Anas*
Mergellus = *Mergus*
Metopiana = *Netta*
Nesochen = *Branta*
Nesonetta = *Anas*
Nomonyx = *Oxyura*
Nyroca = *Aythya*
Oidemia = *Melanitta*
Philacte = *Anser*
Polysticta = *Somateria*
Pseudotadorna = *Tadorna*
Pteronetta = *Cairina*
Salvadorina = *Anas*
Spatula = *Anas*

GENERA RECOGNIZED HERE BUT NOT BY PETERS

Amazonetta von Boetticher (for *Anas brasiliensis*)
Lophonetta Riley (for *Anas specularioides*)

COMPARISON OF CHARACTERS

Our studies have shown that the waterfowl can be divided into about nine groups that are fairly well defined both morphologically and biologically. In addition, there are a number of species and genera that are either intermediate between the otherwise well-defined tribes (e.g. *Coscoroba*) or too poorly known for a safe classification (e.g. *Anas specularis*, *Anas leucophrys*, *Malacorhynchus*, *Tachyeres*); others show peculiarities or a combination of characters that prevent them from fitting well into any of the existing groups. Such genera as the Australian *Cereopsis*, *Anseranas*, *Stictonetta*, and *Chenonetta* could either be made the sole representatives of so many separate tribes or each could be included in the tribe with which it shares the greatest number of similarities. For the sake of convenience we have adopted the latter course, but without forgetting that these genera are not typical representatives of the tribes with which we associate them.

Table 1 lists the more important characters used in our classification of the duck family. Obviously it is impossible in the limited space provided by a table either to describe all characters in detail or to list all the exceptions. The subsequent paragraphs contain some of the information which could not be included in the tabulation.

Morphological Characters

As noted above, one of the most fundamental characters in the duck family is the pattern of the tarsus. All species of the subfamily Anserinae have the front of the tarsus reticulate, but in the Anatinae only the aberrant species *Cereopsis*, *Anseranas*, and *Stictonetta*, all of Australia, show this primitive attribute.

The structure of syrinx and trachea[9] is fairly uniform within each tribe. No special structures are found in the trachea (or syrinx) of the geese, most swans, *Coscoroba*, or *Cereopsis*. The Whooper-Whistling Swan group has the trachea looped through the sternum in both sexes. In *Anseranas* (Cairinini) a large double loop of the trachea is found between the left breast muscle and the skin. This loop is considerably smaller in the female.

The whistling ducks (*Dendrocygna*) have a bulla which consists in an enlargement and ossification of the lower end of the trachea. It is less pronounced n the females.

Most of the Anatinae have strong sexual dimorphism of the vocal apparatus. The male has an asymmetrical bony bulla of the syrinx, big on the left side, small or absent on the right. This structure is absent in the females. Exceptions to this occur in most of the tribes. In *Tadorna tadorna* (and in no other species of this genus) the right bul a is larger than the left. In *Mergus merganser* and *M. serrator* the bulla is exceptionally large. In some Cairinini (e.g. *Sarkidiornis*, and *Plectropterus*), in *Neochen jubatus*, and in two species of scoters it is very small; in *Melanitta nigra* the bulla is absent.

The trachea shows special bulbous inflations among the Anatini (*Anas versicolor*, *Stictonetta naevosa*), the Aythyini (*Netta rufina* and *N. peposaca*), and particularly among the Mergini (*Bucephala*, some species of *Mergus*, *Melanitta*). The bronchi are elongated and inflated in *Melanitta fusca* and in *Somateria*. Oxyurini have no bullae, but their bronchi are inflated; they have curious tracheal or esophageal air sacs. As with all taxonomic characters, the structure of the syrinx sometimes varies independently of the system. This is true particularly in the genera *Cygnus*, *Tadorna*, *Melanitta*, and *Mergus*. Differences in the structure of the syrinx occur in these genera at the species or even at the subspecies level.

[9] The trachea (and syrinx) of many ducks is still unknown. Collectors should therefore save the syrinx of all the specimens to which they have access. The method of preservation is extremely simple. It consists in cutting off the bronchi from the lungs (below the last bronchial ring) and severing the larynx from the throat. The structure should then be submerged in a solution of peroxide (or if that is not available, in alcohol or any other preserving fluid) until bleached, and finally be stretched and mounted by gluing or wiring it against a cardboard. This will protect the structure against breaking after it has dried.

TABLE 1
COMPARISON OF CHARACTERS IN THE ANATIDAE

SUBFAMILY	ANSERINAE		ANATINAE						
TRIBES	ANSERINI	DENDROCYGNINI	TADORNINI	ANATINI	AYTHYINI	CAIRININI	MERGINI	OXYURINI	MERGANETTINI
MOLTS	One		Two (with a few exceptions)						
ADULT PLUMAGE	Usually plain / Elaborate; ♂ like ♀; No speculum		♂ like or unlike ♀; Speculum common		♂ unlike ♀; Nonmetallic speculum	♂ like or unlike ♀; Metallic colors present	♂ very unlike ♀; Nonmetallic speculum common	♂ like or unlike ♀; No speculum	♂ very unlike ♀; Metallic speculum
PATTERN OF DOWNY YOUNG	Faint or absent; White and gray or yellow and brown	Strong, unique; Pale line across nape	Usually bold; White and black (or gray)	Strong. Usually yellowish; Fine eyeline	Eyeline absent or faint	Variable line back of eye	Usually strong; Usually white and black	Indistinct; White and brown (or fuscous)	Distinct; White and black; Dark eyeline; Dorsal spot
FRONT OF TARSUS	Reticulated		Scutellated except in: *Cereopsis*	*Stictonetta*		*Anseranas*			
SYRINX AND TRACHEA	No bulla; Tracheal loop in some *Cygnus*	Small symmetrical bulla in ♂ and ♀	Large asymmetrical bulla in ♂ (except in *Cereopsis*)		(bulla only partly ossified)	(tracheal loop in *Anseranas*)	(variable trachea, often inflated)	No bulla; Enlargements of trachea	Unknown
VOICE	♂ like ♀		♂ unlike ♀. Voice of ♀ often louder						
DISPLAY	Simple. Alike in ♂ and ♀		Unlike in ♂ and ♀. Elaborate pair-formation displays common						
PAIRING. PARENTAL CARE	Pair for life. ♂ shares care of young	♂ (?always) incubates	♂ leaves ♀ when clutch is complete	(except some widgeons)		(no pairing in 2 genera)		Pair for breeding season (?life). ♂ shares care of young	
LOCATION OF NEST	On the ground or:					Holes in trees		On the ground:	
	rarely on ledges or in old nests	sometimes in tree holes	in holes in ground or in trees (1 sp.)	in trees (5 species)		except 2 genera	(or hidden on ground)	in marshes	among rocks and bushes
HABITUAL DIVING	Absent	Present	Absent except in: *Tachyeres*	*Hymenolaimus*	Present	Absent	Present		
CHIEF FOOD	Vegetable except: *Tachyeres*				Varies with season	Vegetable	Animal	Vegetable	Animal

Although the presence or absence of a double molt seems to constitute a first-class criterion of relationship, the presence of a distinct eclipse plumage in males of the double-molting species is of very little significance. Birds inhabiting the colder regions usually have two very different seasonal plumages, while those living in or near the tropics look the same the year round. As in other families, there are, of course, a few exceptions to this rule.

Downy Young

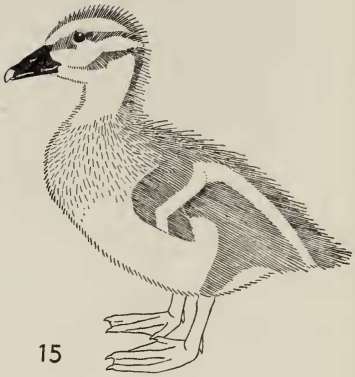
The downy young in most of the nine tribes have a very characteristic pattern and can often be identified as to tribe. Body posture and proportions are also often typical for a tribe. For example, in the Tadornini, and even more in the Cairinini, the insertion of the legs is rather far forward; in the Mergini and particularly in the Oxyurini it is far back. The tails are long in the Cairinini and in most Mergini, and stiffened in the Oxyurini and Merganettini. In the length of the neck and shape of the head there are also characteristic differences between the various tribes. As far as the plumage patterns are concerned, the following short remarks may be useful in conjunction with the semi-diagrammatic drawings (Figures 14–23)[10]. We have refrained from showing the downy young of any of the more common ducks. North American species are figured by Kortright (1942), European by O. and M. Heinroth (1928), in addition to illustrations found in other standard works (Phillips, Witherby, etc.).

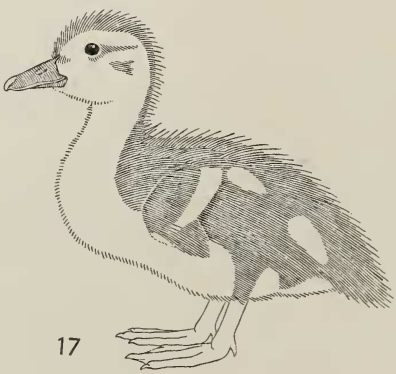
Anserini. Plumage pattern absent or faint. When present (*Branta*), it is similar to that of the Anatini, consisting of two lateral spots on the back. There is occasional indication of a dark stripe through the eye (*Anser*). The ground color is usually white, but it is yellowish in some species of *Branta* and *Anser*.

Dendrocygnini. This tribe is characterized by a light line across the occiput, which extends under the eye to the bill. There is a broad dark line through the eye and a light line above it. There are three or four lateral spots on the upper parts. The ground color is either yellowish (e.g. *autumnalis*) or grayish white (e.g. *guttata*, *bicolor*). The same pattern, though showing only faintly, is found in *Coscoroba*. In *guttata* and *eytoni* (Figures 14 and 15) there is a white stripe along the side of the back.

Tadornini. Birds of this tribe are characterized by a conspicuous pattern with sharp contrast (Figures 9 and 10). The upper parts are dark (black or gray), sometimes forming a cap on the head (Figure 16. *Tadorna ferruginea*). There are bold white spots on wing and back, often fusing into a longitudinal stripe. In *Chloëphaga* there is great

[10] The excellent semi-diagrammatic illustrations of the downy young were drawn by Alexander Seidel whose services we gratefully acknowledge.





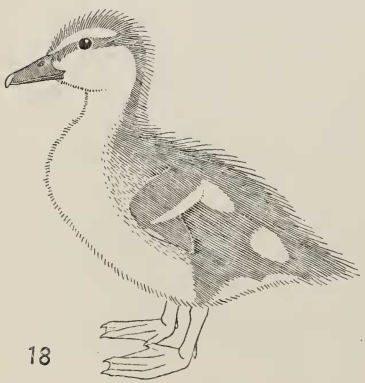


Figure 14. Spotted Whistling Duck, *Dendrocygna guttata.*
Figure 15. Plumed Whistling Duck, *Dendrocygna eytoni.*
Figure 16. Ruddy Sheldrake, *Tadorna ferruginea.*
Figure 17. Salvadori's Duck, *Anas waigiuensis.*
Figure 18. Ringed Teal, *Anas leucophrys.*

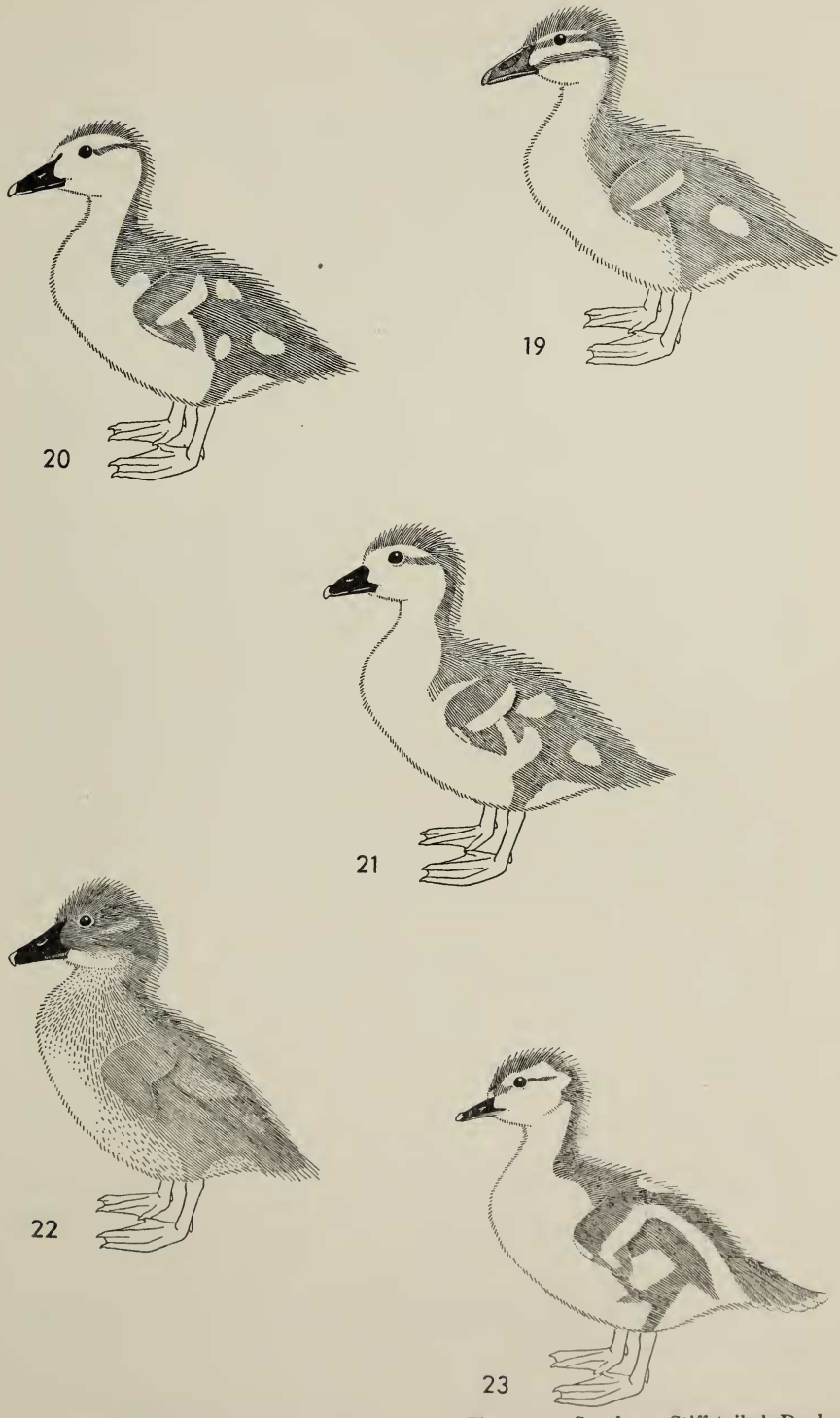


Figure 19. Maned Goose, *Chenonetta jubata.*
Figure 20. Muscovy Duck, *Cairina moschata.*
Figure 21. Spur-winged Goose, *Plectropterus gambensis.*

Figure 22. Southern Stiff-tailed Duck, *Oxyura australis australis.*
Figure 23. Torrent Duck, *Merganetta armata colombiana.*

variability. Broad white superciliary stripes narrow the dark crown in *picta* to a medial stripe from bill to back. The downy young in *Cereopsis* (Figure 7) is very similar, but it has a black facial mask and very little white on the wing.

Anatini. There is great uniformity of pattern in this tribe, the downy young of all species resembling more or less those of the Mallard. There are two lateral spots on the back, and the ulnar edge of the wing is light. A dark line through the eye is apparently always present, though sometimes interrupted as in *Anas waigiuensis* (Figure 17). Although the adult of *Anas leucophrys* shows many striking peculiarities, the downy young (Figure 18) is much like those of typical species of *Anas*. The ground color is usually pale yellow or yellowish-cinnamon, rarely whitish.

Aythyini. The basic pattern of the downy young of the pochard tribe is similar to that of the Anatini. The yellow wash is usually much stronger, and the dark line through the eye inconspicuous or absent. Young scaup are rather dark, and the size of the spots on the back is reduced. Young Tufted Ducks are blackish.

Cairinini. All perching ducks have a contrasting pattern which is in general fairly similar to that of the Anatini but varies from species to species. There is a very variable dark stripe from the eye to the nape. In *Chenonetta* (Figure 19) and *Aix galericulata* there are two parallel dark lines across the face. There is some white at the ulnar edge of the wing and usually two or three rather small lateral light spots on the back. The ground color is usually yellow, sometimes white (*Nettapus*). The downy young in *Sarkidiornis*, *Cairina* (Figure 20), and *Plectropterus* (Figure 21) are similar to one another.

Mergini. Two major plumage patterns are found among the downy young of this family. The eiders (*Somateria*) have a simplified plumage, dull gray-brown above with white breast and belly. Common and Surf Scoters are similar, but more blackish, with an indication of white cheeks and of a dark cap. The White-winged Scoter, Old-squaw, and Harlequin lead to the typical *Bucephala* pattern. It is boldly black and white. A blackish cap, extending to a line well below the eye, contrasts with the white cheeks. The ulnar edge of the wings and two or three lateral spots on the back are white. The mergansers (*Mergus*) are essentially similar, except that the sides of the face are washed with rufous. Some have a light superciliary.

Oxyurini. The stiff-tailed ducks have a rather aberrant pattern of down; it is indistinct, brownish (or fuscous) and white. (Figure 22. *Oxyura australis.*)

Merganettini. The downy young of *Merganetta* is black and white with a dark line through the eye. It is unique in having long tail

feathers and a central white spot on the back. The pattern gives no clue to the relationship. (Figure 23. *Merganetta armata colombiana.*)

Biological Characters

Biological characters are of paramount importance to the classifier, for habits and behavior are certainly deeply rooted and are often the product of a very ancient evolution. In the present family the main points are pair formation, displays, nesting, and feeding habits.

Pair formation and parental care. The pair is a well-knit unit in the Anserini, Dendrocygnini, and Tadornini. In all three tribes the two sexes seem to pair for life, both mates share in the raising of the young, and in some species (*Dendrocygna*, *Cygnus atratus*) the male participates even in incubation. In the stiff-tailed ducks (Oxyurini) and certain widgeons, the male helps in raising the young, but it is as yet unknown whether or not the two sexes are paired for life. In most of the ducks (e.g. most Anatini, all Aythyini, most Cairinini, and all Mergini), male and female pair only for the nuptial season. The drake leaves the duck soon after the beginning of incubation. Random fertilization without pair formation seems to occur among certain genera of Cairinini (*Cairina*, *Sarkidiornis*). Merganettini appear to live in pairs, both sexes taking care of the young.

Courtship and displays. The chronology and significance of display in the Anatidae are still not well known. Roughly there are three main phases of courtship: (a) The prenuptial or pair-formation period. During this period one usually sees small troupes of males perform before one or several females. Finally a single male and female become paired and separate from the rest of the flock. (b) The nuptial period. During this period, which lies between pair formation and egg laying, there is commonly less display. The individual display postures are usually the same as in Phase *a*. Among the Anatini, Aythyini, Oxyurini, the pair-forming Cairinini, and most of the Mergini, the males have elaborate display postures, which, particularly during Phase *b*, are usually answered in a simplified manner by the female. The female often takes the initiative in the display of certain Tadornini, while among certain Cairinini there is no regular display, but merely a pursuit of females by males. (c) Sexual period. Copulation is preceded among swans, geese, and certain ducks by rather elaborate preparatory performances.

Hochbaum (1944) may be consulted for an excellent description and analysis of the phases of courtship among the migratory species of the northern hemisphere, which do not mate for life. Different sequences exist in species that pair for life, in sedentary species which pair on the breeding territory, and in non-pairing species such as Muscovies. However, little accurate information on these is available.